

THE CAUDAL SKELETON IN MESOZOIC ACANTHOPTERYGIAN FISHES



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SYNOPSIS

This paper contains descriptions of the caudal skeleton in all Ctenothrissiformes and Mesozoic acanthopterygians, comparisons with living relatives being made where possible, and a brief account of the caudal skeleton in Mesozoic Myctophoidei. These groups have a basically similar caudal skeleton with the first ural and pre-ural centra fused, the second ural centrum free, six hypurals, three epurals, a stegural and a second uroneural. Caudal scutes persist in Ctenothrissiformes and primitive Myctophoidei and there is a single urodermal in some Cretaceous myctophoids.

The bearing of caudal structure on the origin and early evolution of acanthopterygians is discussed and variations in the second pre-ural neural spine are shown to be important. This structure is primitively short and slender: two opposite developments from this condition are elongation of the spine to support procurrent fin-rays (as in Polymixioidei) and reduction to a low crest (as in Berycoidei and Perciformes). Wherever a full second pre-ural neural spine occurs in perciform and higher groups it is produced secondarily by fusion with the first epural. The evidence of the caudal skeleton does not support a polyphyletic origin of Perciformes from different groups of Beryciformes. The Berycoidei appear to be the beryciform group most closely related to the Perciformes.

The Danian *Bathysoma* is shown to be a lampridiform: the lampridiforms probably arose from near *Aipichthys* and *Pharmacichthys*. The Zeiformes are close relatives of the Berycoidei.

I. INTRODUCTION

In an earlier paper (Patterson 1964) I gave detailed accounts of the skeletal anatomy of the known Mesozoic acanthopterygian fishes (see also Patterson 1967) but without describing the caudal skeleton. This was omitted because when the bulk

of the work was done there existed no comprehensive description or even terminology of the caudal skeleton of living teleosts. But during the last few years, following from the work of Gosline (1960), the caudal skeleton has become recognized as an important structure in tracing the relationships of teleost fishes and we now have both a satisfactory terminology (Gosline 1960; Nybelin 1963; Monod 1967; Patterson 1968) and a reasonable idea of the composition of the caudal skeleton in most teleostean groups (Gosline 1960, 1961, 1961a, 1963, 1965; Norden 1961; Rosen 1962, 1964; Greenwood, Rosen, Weitzman & Myers 1966; Monod 1967; Greenwood 1967; Weitzman 1967). In the light of this new information it seemed that an investigation of the caudal skeleton in Mesozoic acanthopterygians might prove a useful check on hypotheses of the origins of acanthopterygians and paracanthopterygians (Greenwood *et al.* 1966). Also included are accounts of caudal structure in the Ctenothrissiformes and, more briefly, in the Mesozoic Myctophoidi.

The terminology used here is that of Nybelin (1963) with the distinction between "urodermal" and "uroneural" introduced by Patterson (1968) and the addition from Monod (1967) of the terms "parhypural", for the haemal arch of the first pre-ural centrum, the terminal structure perforated by the caudal vein and artery and which bears the hypurapophysis (Nursall 1963), and "stegural" for the paired structure which articulates with the dorso-lateral surface of the first pre-ural centrum and has a slender shaft extending postero-dorsally, lateral to the nerve cord. Monod considers the stegural to be an element *sui generis*, not a compound structure. In my opinion (Patterson 1968), the stegural represents the first uroneural fused with neural arch material from the first pre-ural and first ural vertebrae. The term stegural is nevertheless useful, since it obviates repetition of the cumbersome term "first uroneural fused with the neural arches of the first ural and pre-ural centra".

The material used is mainly in the collections of the British Museum (Natural History): these specimens are referred to by a registered number without prefix or with the prefix "P". Specimens from the American University, Beirut, the American Museum of Natural History, New York, the Royal Scottish Museum, Edinburgh, and the United States National Museum, Washington, are referred to with the prefixes "AUB", "AMNH", "RSM" and "USNM" respectively. The illustrations of fossil species are not reconstructions but *camera lucida* drawings of single specimens.

I am grateful to Drs. P. H. Greenwood and D. E. Rosen, who have read and criticized parts of this paper in manuscript, and for the loan of specimens to Prof. T. Raven, American University, Beirut, Drs. C. D. Waterston and R. S. Miles, Royal Scottish Museum, Dr. Bobb Schaeffer, American Museum of Natural History, and Drs. D. H. Dunkle and D. M. Cohen, United States National Museum.

II. SYSTEMATIC DESCRIPTIONS

Order CTENOTHRISSIFORMES (Patterson 1964 : 218)

According to Marshall (1961) the living *Macristium chavesi* is a surviving ctenothrissiform (see also Greenwood, Rosen, Weitzman & Myers 1966; Patterson 1967 : 86). Unfortunately, the only extant specimen of *Macristium* is a post-larval

individual and the caudal skeleton is not ossified. But there appear to be six hypurals, as in Ctenothrissiformes. Berry & Robins (1967) have described a second macristiid, *Macristiella perlucens*, known only by a single post-larval specimen. In this fish there are six hypurals, as in Ctenothrissiformes, but Berry & Robins think it unlikely that the Macristiidae are close to the Ctenothrissiformes.

Family **AULOLEPIDIDAE** Patterson (1964 : 247)

Genus **PATEROPERCA** Smith Woodward (1942 : 543)

The type and only species, *P. libanica* Smith Woodward from the Middle Cenomanian of Hajula, Lebanon, is known only by two specimens, AUB 108906 (the holotype) and AUB 108904. In 108904 the caudal region is badly preserved and yields no useful information, but in the holotype the caudal skeleton is very well preserved (Fig. 1). The second pre-ural centrum (*pu2*) has a fully developed neural spine (*npu2*) and an autogenous haemal arch. It is not possible to see with certainty whether the haemal arch of the third pre-ural centrum (*pu3*) is autogenous. The first pre-ural and first ural centra are fused (*pu1 + u1*), these fused centra bearing the parhypural (*ph*) and the first and second hypurals (*h1*, *h2*) in the normal way. The first hypural is rather slender, only a little broader than the parhypural and

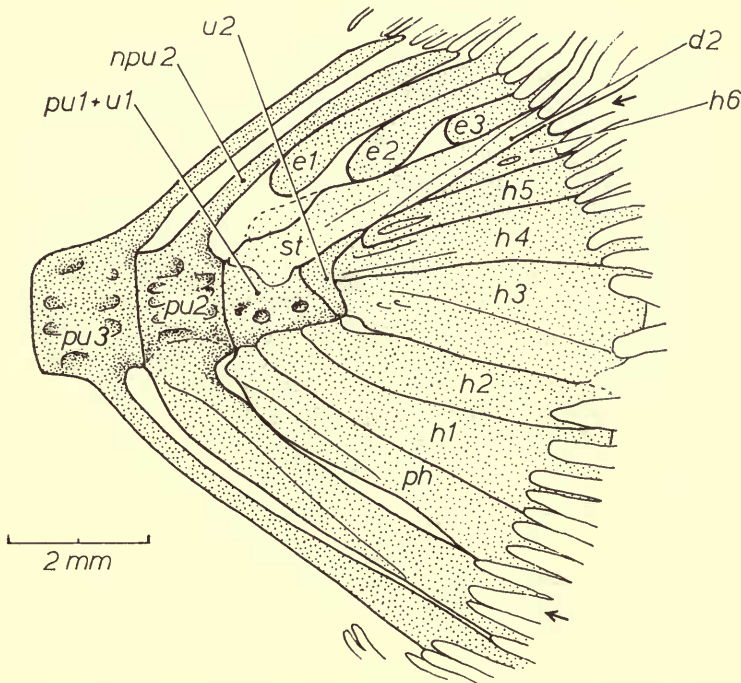


FIG. 1. *Pateroperca libanica* Smith Woodward. Caudal skeleton of the holotype, AUB 108906, standard length 86 mm., Middle Cenomanian, Hajula, Lebanon. For explanation of lettering see p. 102. Arrows mark the outermost (unbranched) principal fin-rays.

the second. Dorsally, the fused first pre-ural and ural centra bear a large stegural (*st*) and there is a second uroneural (*d2*) ending, as usual, in front of the base of the first unbranched principal ray of the caudal fin. There are three epurals (*e1* — 3), the third small and short. There is a small independent second ural centrum (*u2*) bearing three hypurals (*h3* — 5) decreasing in size upwards, and above these there is a small sixth hypural (*h6*) which probably failed to make contact with the ural centrum. The foremost procurent rays of the caudal fin, which are unsegmented lepidotrichia, not spines, are inserted in front of the neural and haemal spine of the third pre-ural centrum. The uppermost principal ray of the fin (unbranched) is preceded by nine rays, only the last two or three segmented, and the lowermost by seven rays, the last two segmented.

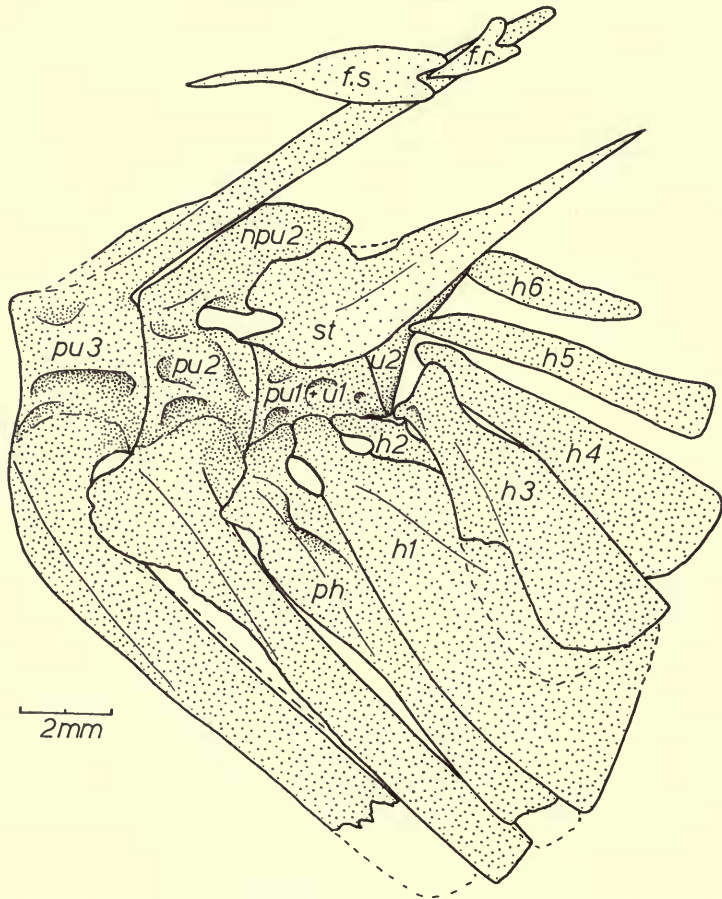


FIG. 2. *Aulolepis typus* Agassiz. Caudal skeleton of 47932, standard length *c.* 165 mm., Lower Chalk, Burham, Kent. *f. r.*, foremost procurent fin-ray (displaced); for explanation of other lettering see p. 102. The upper hypurals are displaced ventrally, the epurals and second uroneural are missing.

Genus *AULOLEPIS* Agassiz (1844 : 109)

In the type and only species, *A. typus* Agassiz from the Upper Cenomanian of the English Chalk, only two specimens show any details of the caudal skeleton, 4033 (the holotype, Fig. 3) and 47932 (Fig. 2), and in both the bones are disturbed to some extent. The caudal skeleton of *Aulolepis* agrees with that of *Pateroperca* in most respects: fusion of the first pre-ural and first ural centra ($pu1 + u1$), presence of a free second ural centrum ($u2$), three epurals ($e1 - 3$), six hypurals ($h1 - 6$) of which the first and the third are largest, an autogenous haemal arch on the second pre-ural centrum ($pu2$), a stegural (st) and a free second uroneural ($d2$). The haemal arch of the third pre-ural centrum ($pu3$) appears to be autogenous in 47932 but fused with the centrum in 4033. *Aulolepis* differs clearly from *Pateroperca* in having the neural spine of the second pre-ural centrum developed as a low, broad crest ($npu2$) whose hind edge fits between the front edges of the stegurals. In my earlier descriptions of *Aulolepis* and *Pateroperca* (Patterson 1964 : 247) I discussed the difficulty of separating the two genera and considered the possibility that *P. libanica* is merely

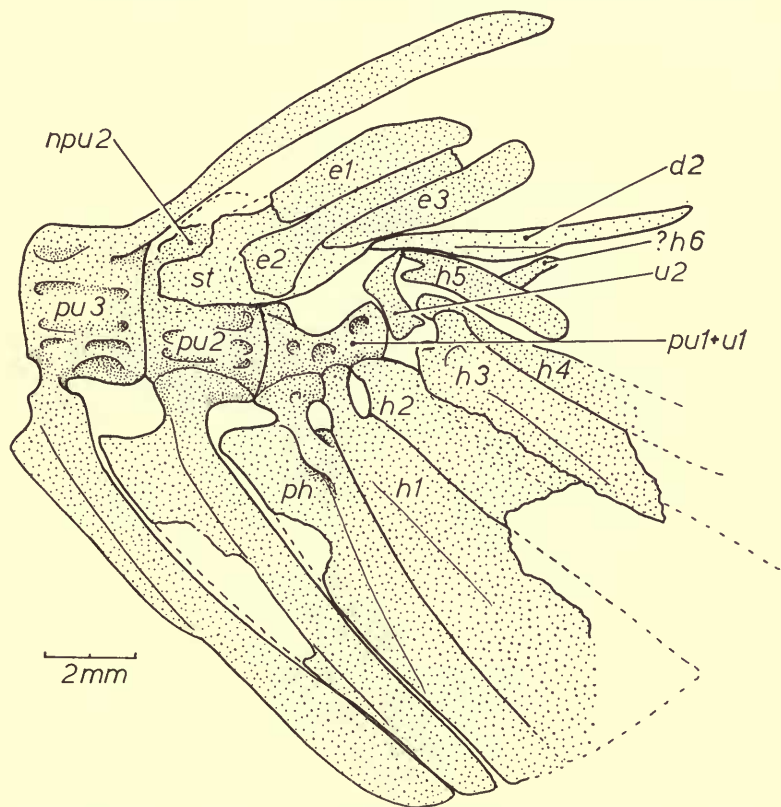


FIG. 3. *Aulolepis typus* Agassiz. Caudal skeleton of the holotype, 4033, standard length c. 135 mm., Lower Chalk, Lewes, Sussex. For explanation of lettering see p. 102. The epurals and upper hypurals are displaced ventrally, the stegural is displaced forwards.

a species of *Aulolepis*, but the presence on the second pre-ural centrum of a fully developed neural spine in *Pateroperca* and of a low crest in *Aulolepis* clearly separates the two genera. The caudal of 47932 shows one other point of interest, a slender, elongated caudal scute (*f. s.*, Fig. 2) in front of the upper lobe of the fin. There is no conclusive evidence of a similar structure in front of the lower lobe of the fin, but it was probably present since there is a caudal scute in front of each lobe of the fin in *Ctenothrissa* (see below) and in most living teleosts which still retain these structures (*Elops*, *Tarpon*, *Albula*, *Aulopus* and *Chanos*, Gosline 1965 : 192; *Argentina*, Weitzman 1967 : 532). There is no sign of caudal scutes in either specimen of *Pateroperca*, but again it is probable that they were present. No specimen of *Aulolepis* has the fin-rays of the caudal fin well preserved but 4033 shows that the foremost procurrent rays of the lower lobe articulated with the haemal spine of the third pre-ural centrum, and both 4033 and 47932 show that these foremost rays were true spines.

Family CTENOTHRISSIDAE Smith Woodward (1901)

Genus CTENOTHRISSA Smith Woodward (1899 : 490)

In *Ctenothrissa*, the only genus of the Ctenothrissidae, the caudal skeleton and fin are well exposed in the two species from the Cenomanian of the Lebanon, *C. vexillifer*

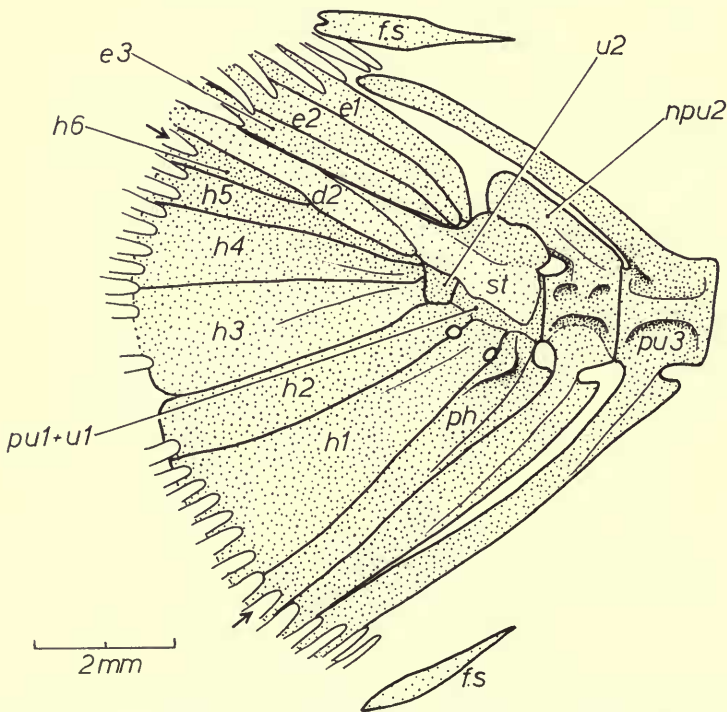


FIG. 4. *Ctenothrissa signifer* Hay. Caudal skeleton of P. 47524, standard length 83 mm., Middle Cenomanian, Hajula, Lebanon. For explanation of lettering see p. 102. Arrows mark the outermost (unbranched) principal fin-rays.

(Pictet 1850), the type species, and *C. signifer* Hay (1903) (Fig. 4), and the caudal skeleton is preserved in one or two specimens of *C. microcephala* (Agassiz) (Fig. 5) and *C. radians* (Agassiz) from the Upper Cenomanian of the English Chalk. There seem to be no significant differences in caudal anatomy between these four species. As in Aulolepididae, there is a free second ural centrum (u_2), the first ural and first pre-ural centra are fused ($pu_1 + u_1$), there are six hypurals ($h_1 - 6$), the first and third the largest and the sixth failing to articulate with the second ural centrum, there are three epurals ($e_1 - 3$), a stegural (st) and a second uroneural (d_2) and the haemal arch of the second pre-ural centrum (pu_2) is autogenous. The haemal arch of the third pre-ural centrum (pu_3) appears partially or completely fused to the centrum. As in *Aulolepis*, but in contrast to *Pateroperca*, the neural spine of the second pre-ural centrum (npu_2) is represented by a broad crest, about half as high as the preceding spine. There is a slender caudal scute ($f. s.$) in front of both the upper and lower lobes of the caudal fin. In *C. vexillifer* and *C. signifer*, the only species in which the caudal fin-rays are well preserved, both the upper and lower principal rays are preceded by six rays, the last two segmented, and the foremost fin-rays are inserted on the neural and haemal spines of the third pre-ural centrum.

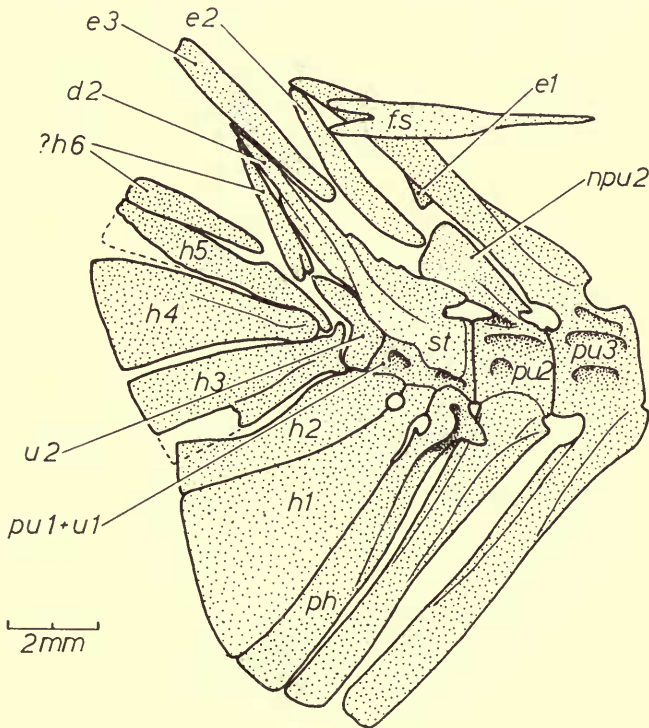


FIG. 5. *Ctenothrissa microcephala* (Agassiz). Caudal skeleton of 49881, standard length c. 115 mm., Lower Chalk, zone of *Holaster subglobosus*, Reigate, Surrey. For explanation of lettering see p. 102. The upper hypurals are displaced ventrally. Of the two elements labelled ? h_6 , that on the left may be the base of a fin-ray.

In these small species from the Lebanon, the foremost procurent caudal rays are unsegmented lepidotrichia, with separate right and left halves, but in the larger species from the English Chalk they appear to be true spines.

Order BERYCIFORMES

Suborder POLYMIXIOIDEI Patterson (1964 : 433)

Family **POLYMIXIIDAE** Gill (1862)

The only living genus of this family and suborder is *Polymixia*. The caudal skeleton of *Polymixia nobilis* has been figured by Regan (1911, fig. 1) and briefly discussed by Gosline (1961 : 14). The specimen illustrated here (Fig. 6) is almost certainly that used by Regan. The haemal arches of the second and third pre-ural centra (*pu2*, *pu3*) are autogenous, the second pre-ural centrum has a fully developed neural spine (*npu2*), the first pre-ural and first ural centra are fused (*pu1 + u1*) and there is a free second ural centrum (*u2*). There is a large stegural (*st*) and a free second uroneural (*d2*). There are three slender epurals (*e1 - 3*) and six hypurals (*h1 - 6*) of which the first and the fourth are the largest, the third being excavated posteroventrally to give a notch between the hypurals supporting the upper and lower lobes of the fin. The second ural centrum has a long posterior process and makes contact with the sixth hypural. The first rays of the caudal fin articulate with the neural and haemal spines of the third pre-ural centrum. In the upper lobe of the fin the first unbranched principal ray is preceded by four true spines and two

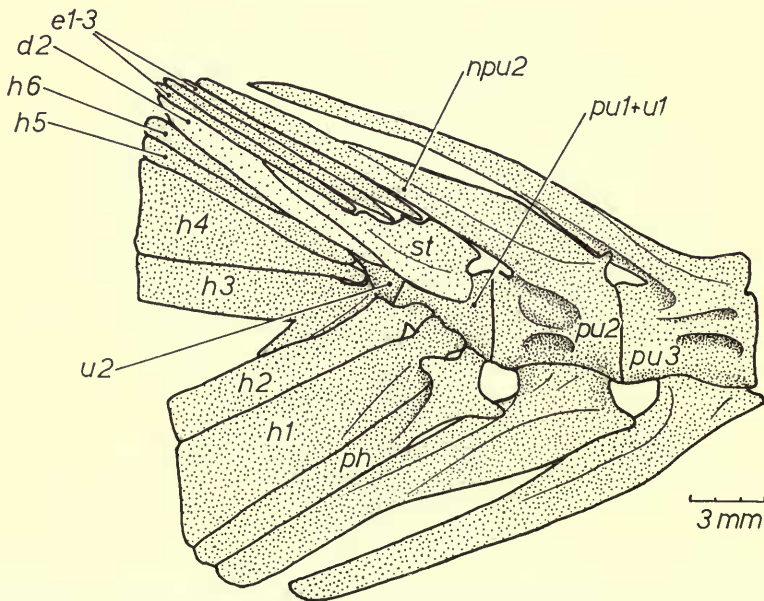


FIG. 6. *Polymixia nobilis* Lowe. Caudal skeleton of a dried skeleton, 1895.5.28.1, standard length 220 mm., Madeira. For explanation of lettering see p. 102.

segmented rays, in the lower lobe by three spines and two segmented rays. A caudal skeleton of *P. japonicus* does not differ from that of *P. nobilis*.

Genus *BERYCOPSIS* Dixon (1850 : 372)

In the type species, *B. elegans* Dixon from the Upper Cenomanian and Turonian of the English Chalk, the caudal skeleton is well preserved in 25881 (Fig. 7) and P.6465. The caudal skeleton of *B. elegans* agrees with that of *Polymixia* in almost every detail except that the third hypural (*h3*) is not excavated postero-ventrally so that it is as large as the fourth, the haemal arch of the third pre-ural centrum, probably autogenous in P.6465, is fused with the centrum in 25881, and the third and fourth hypurals, separate in 25881 (standard length *c.* 13 cm.), are completely fused in the larger P.6465 (standard length *c.* 16 cm.). In 25881 the lateral surface of the second ural centrum is covered by a small, triangular plate (*x*, Fig. 7). P.6465 is not sufficiently well preserved to see whether this plate is present. The plate appears to be part of the caudal skeleton, not a dermal element which has become apposed to the centrum *post mortem*. The only record of a similar structure is in the living myctophoid *Synodus foetens*, where Hollister (1937a, figs. 5, 12) found a "uroneural" in this position, ventral to the normal uroneurals. The foremost

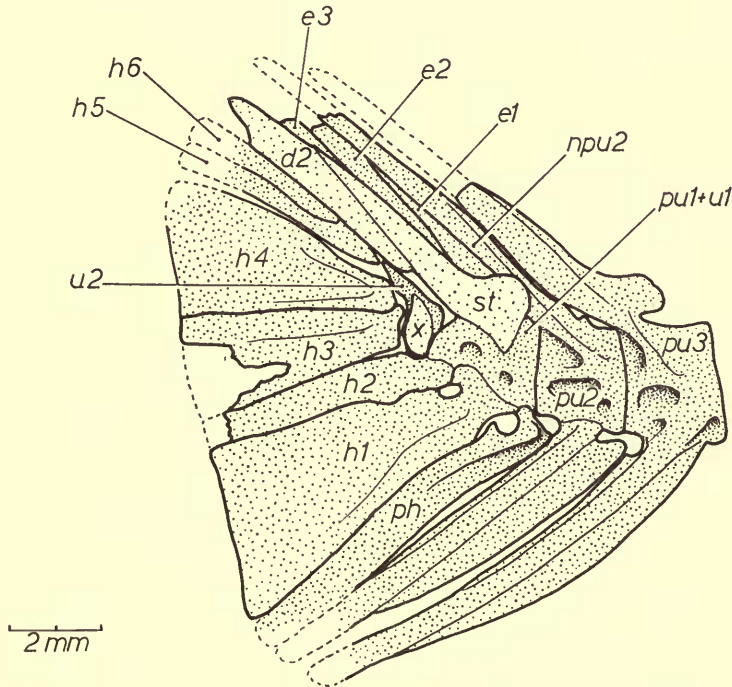


FIG. 7. *Berycopsis elegans* Dixon. Caudal skeleton of 25881, standard length *c.* 130 mm., Chalk, Sussex. *x*, unidentified plate covering second ural centrum; for explanation of other lettering see p. 102.

unsegmented caudal fin rays of *B. elegans* are soft rays, not spines as they are in *Polymixia*.

Of P. 10471, a small fish lacking the head, I rashly stated that it is "certainly *B. elegans*" (Patterson 1964 : 278), but on re-examining this specimen I find that the scales are larger than in *B. elegans*, the dorsal and anal spines are longer, there are five anal spines (not four as stated earlier) and in the caudal skeleton the neural spine of the second pre-ural centrum is much reduced. This specimen is clearly not *B. elegans* and the reduced neural spine of the second pre-ural centrum shows that it is not even a polymixioid, but there is insufficient evidence to decide on its real position.

The second species of *Berycopsis*, *B. germanus* (Agassiz) from the Campanian of Westphalia, shows nothing in the caudal skeleton to distinguish it from *B. elegans* except that the haemal arch of the third pre-ural centrum is clearly autogenous and there is no sign of fusion between the third and fourth hypurals in the two specimens where this region is visible. *B. germanus* is so preserved that it shows the details of the caudal fin-rays much better than *B. elegans*. The foremost rays of the caudal fin are arranged asymmetrically, the upper rays articulating with the neural spine of the second pre-ural centrum, the lower with the haemal spine of the third pre-ural centrum. The first principal ray (unbranched) of the upper lobe is preceded by four unsegmented and one segmented ray, the lower by three unsegmented and one segmented ray. It is not possible to see whether the foremost rays are spines (as in *Polymixia*) or soft rays, as in *B. elegans* and *Omosoma*.

Genus *OMOSOMA* Costa (1857 : 106)

Having now had the opportunity to make a direct comparison between the holotypes of *Omosoma pulchellum* (Davis 1887) (RSM 1891.59.72) and *O. intermedium* Smith Woodward (1901) (48112) I find that the two are conspecific, the median fin counts (D V, 28-30; A III-IV, 24) being the same in both. The apparent differences in proportions of the two (Smith Woodward 1901 : 420) are due to longitudinal compression of the holotype of *O. pulchellum*, the holotype of *O. intermedium* showing the true proportions of the fish. In my earlier description of *Omosoma* (Patterson 1964 : 374) the median fin counts given for *O. pulchellum* (D IV-V, 35; A III-IV, 29) were based on distorted specimens of *O. sahelalmae*. *O. intermedium* is therefore a synonym of *O. pulchellum*.

None of the specimens of *Omosoma* available, belonging to *O. sahelalmae* Costa (the type species) and *O. pulchellum* (Davis), from the Upper Santonian of Sahel Alma, Lebanon (Ejel & Dubertret 1966, have recently found evidence of the precise age of these beds), has the caudal skeleton sufficiently well preserved to be illustrated, but all give a picture of a caudal skeleton which does not differ significantly from that of *Berycopsis*. The foremost rays of the caudal fin are arranged asymmetrically, those of the upper lobe articulating with the neural spine of the second pre-ural centrum, those of the lower lobe with the haemal spine of the third pre-ural centrum, just as in *B. germanus*. In both the lobes of the fin there are 4 unsegmented lepidotrichia (not spines) and two segmented rays in front of the principal rays.

It is impossible to see whether the haemal arch of the third pre-ural centrum is autogenous.

Genus *PYCNOSTERINX* Heckel (1849 : 337)

Pycnosterinx is known by four species, all from the Upper Santonian of Sahel Alma, Lebanon. Figure 8 shows the caudal skeleton of *P. russeggerii* Heckel, the type species: it is very similar to those of the other polymixiids and differs from *Polymixia* (Fig. 6) only in having the postero-ventral part of the third hypural completely ossified, so that there is no gap between the hypurals supporting the upper and lower lobes of the fin. As in *Polymixia* the neural and haemal spines are strongly inclined and the epurals slender. As in *Berycopsis* and *Omosoma*, but in contrast to *Polymixia*, the foremost caudal fin-rays are arranged asymmetrically, the upper ones articulating with the neural spine of the second pre-ural centrum, the lower with the haemal spine of the third pre-ural centrum. In both the upper and lower lobes of the fin the principal rays are preceded by three unsegmented soft rays and three segmented rays. *P. discoides* Heckel and *P. gracilis* Davis do not differ in caudal structure from *P. russeggerii* except that in *P. gracilis* there appear to be only five procurrent rays. I have seen no specimens of *P. dubius* Davis in which the caudal skeleton and fin are well preserved, but in the holotype of *Pycnosterinx latus* Davis (1887 : 534, pl. 27, fig. 2), RSM 1891.59.77 (referred to as a "fragmentary fish of indeterminable genus" by Smith Woodward 1901 : 395), the scales have the same spinous surface as in *P. dubius* (Patterson 1964 : 380) and it is probable that the specimen is a large, distorted individual of *P. dubius*, although the state of

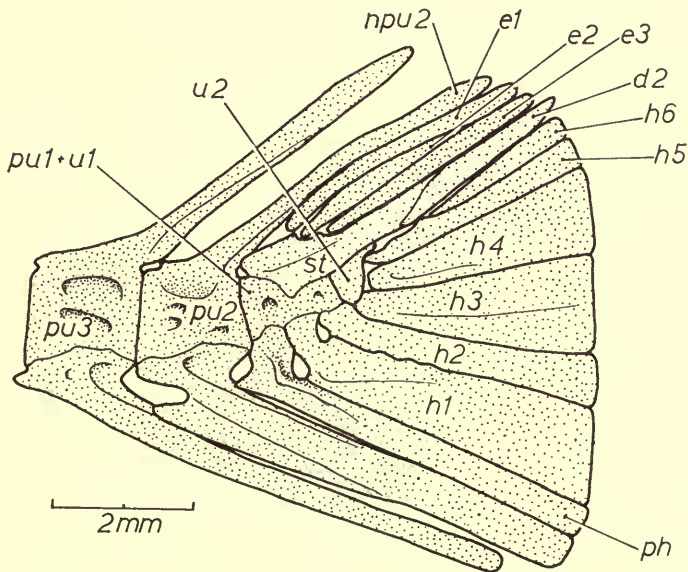


FIG. 8. *Pycnosterinx russeggerii* Heckel. Caudal skeleton of 47820, standard length 78 mm., Upper Santonian, Sahel Alma, Lebanon. For explanation of lettering see p. 102.

preservation of this and the holotype of *P. dubius* is such that this cannot be demonstrated with sufficient certainty to synonymize the two species. *P. latus* appears to have one or two more anal fin-rays and caudal vertebrae than the holotype of *P. dubius*. The caudal skeleton is completely exposed in the holotype of *P. latus* and does not differ from that of *P. russeggerii* in any way, but both in this specimen and in *P. dubius* the foremost fin-rays are true spines, a difference from the other species of *Pycnostrinx* and a resemblance to the living *Polymixia*.

Genus *HOMONOTICHTHYS* Whitley (1933 : 146)

All three species of this genus occur in the Upper Cenomanian—Lower Turonian of the English Chalk. In the type species, *H. dorsalis* (Dixon), only one specimen, 43575, shows anything of the caudal skeleton and here it is only possible to see that there was a fully developed neural spine on the second pre-ural centrum and that the foremost rays of the upper caudal lobe are true spines, articulating with the neural spine of the third pre-ural centrum. In these last two features *H. dorsalis*

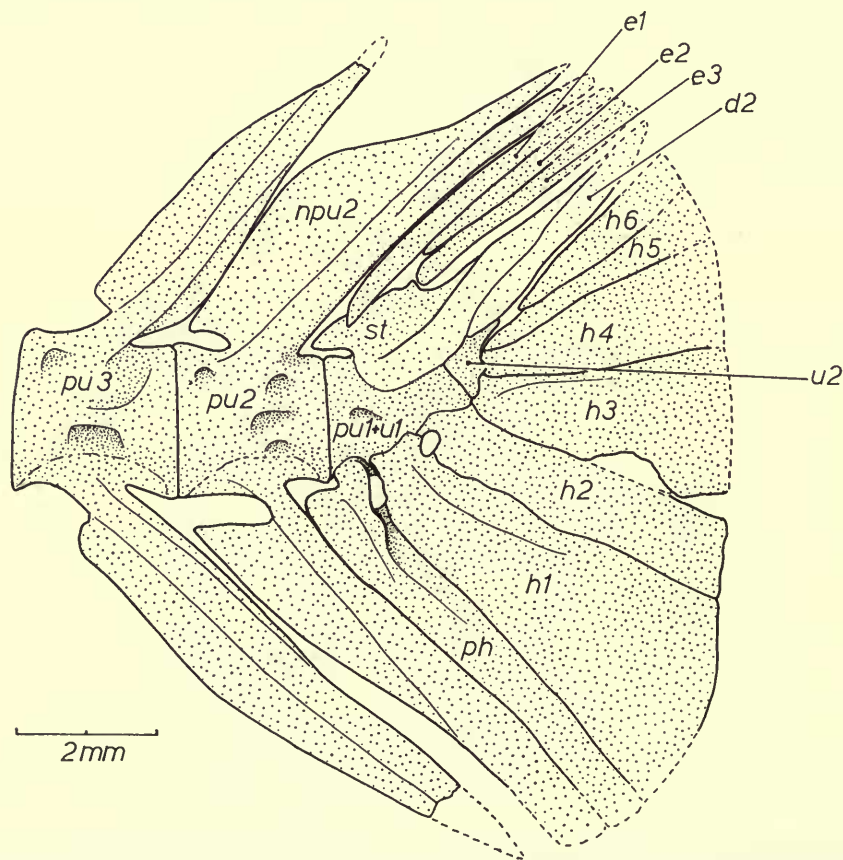


FIG. 9. *Homonotichthys pulchellus* (Dixon). Caudal skeleton of P. 11112, standard length c. 110 mm., Lower Chalk, Amberley, Sussex. For explanation of lettering see p. 102.

resembles *Polymixia* and differs from other Cretaceous polymixiids except *Pycnosterinx dubius*.

In *H. pulchellus* (Dixon) the caudal skeleton is preserved in the holotype, 25886, and in two specimens only recently recognized as belonging to this species, P.11112 (Fig. 9) and P.10639; the latter are about 110 and 120 mm. respectively in standard length, the largest examples of this species yet recorded. The caudal skeleton of P.11112 (Fig. 9) is abnormal in the partial doubling of the neural spine of the second pre-ural centrum and in having the second epural smaller than the third. The caudal skeleton of *H. pulchellus* is very like that of *Polymixia*, with autogenous haemal arches on the second and third pre-ural centra (pu_2 , pu_3) six hypurals ($h_1 - 6$), three slender epurals ($e_1 - 3$), a free second ural centrum (u_2), a stegural (st) and a second uroneural (d_2). The postero-ventral corner of the third hypural is truncated, but less so than in *Polymixia*. Broad flanges on the anterior margin of the neural spines of the second and third pre-ural centra are characteristic of *H. pulchellus*. All three specimens show that the foremost caudal rays are spines, as in *H. dorsalis* and *Polymixia*. In P.10639 the caudal rays articulate with the neural and haemal spines of the third pre-ural centrum, as in *Polymixia*. In P.11112 where the second pre-ural spine is abnormal, the foremost upper caudal rays articulate with the neural spine of the second pre-ural centrum. The lowermost principal caudal ray (unbranched) is preceded by four spines and three segmented rays. P.11112 shows the anal fin of *H. pulchellus*, previously unknown. The fin contains five spines, the first very small and the fifth the longest and thickest, and about eleven soft rays. The fifth anal spine is equal in length to the longest dorsal spine, just over one-quarter of the maximum depth of the trunk.

H. rotundus (Smith Woodward) is known only by the holotype, P.315, and P.5682. P.5682 shows most of the details of the caudal skeleton: there is nothing to distinguish it from the other polymixiids described here except that there is no flange on the anterior margin of the neural spine of the second pre-ural centrum as there is in *H. pulchellus*. P.315 shows that the foremost caudal rays are soft rays, longitudinally divided, not spines as they are in *H. dorsalis*, *H. pulchellus* and *Polymixia*. These two points may be added to others (Patterson 1964 : 299) indicating that this species is incorrectly placed in *Homonotichthys*, but more specimens are necessary before its true position can be decided.

Family SPHENOCEPHALIDAE Patterson (1964 : 383)

The only member of this family is *Sphenocephalus fissicaudus* Agassiz from the Campanian of Westphalia. Of the six specimens in the British Museum (Natural History), three, P.2100 (Fig. 10), P.8772 and P.9059 have the caudal skeleton well preserved. As in Polymixiidae, the second pre-ural centrum has a fully developed neural spine (npu_2), there is a free second ural centrum (u_2), a stegural (st), a second uroneural (d_2), and six hypurals ($h_1 - 6$). As in *Polymixia*, the foremost procurrent rays articulate with the neural and haemal spines of the third pre-ural centrum. In contrast to all Polymixiidae there are only two epurals (e_1 , 2), the first curved forwards proximally and with a gap between it and the neural spine of the second

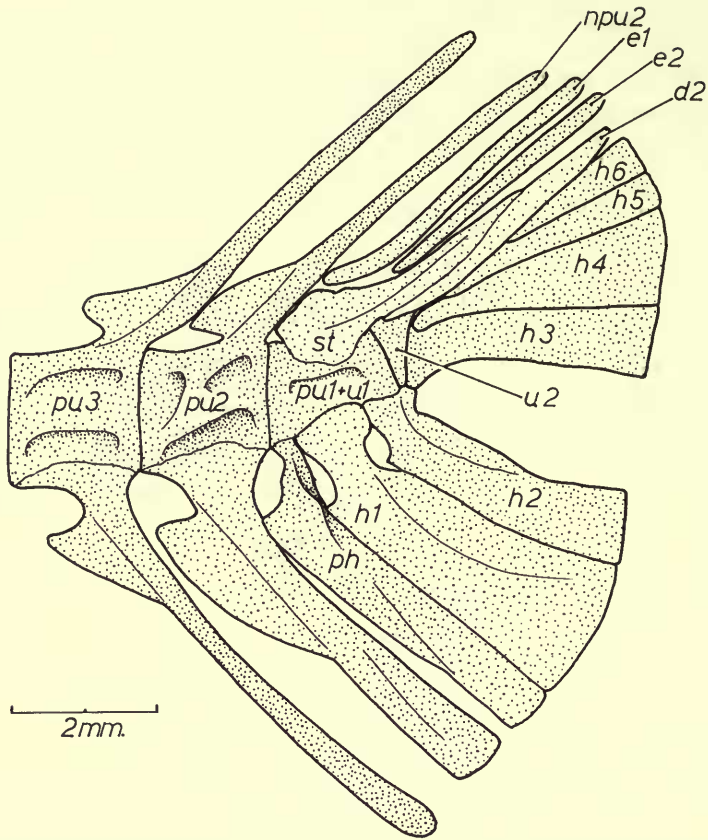


FIG. 10. *Sphenocephalus fissicaudus* Agassiz. Caudal skeleton of P. 2100, standard length 92 mm., Campanian, Sendenhorst, Westphalia. For explanation of lettering see p. 102.

pre-ural centrum, there is a wide gap between the upper and lower hypurals, and there is a large number of procurrent rays, apparently nine in each lobe, six unsegmented soft rays and three segmented in the upper, five unsegmented and four segmented in the lower.

Suborder DINOPTERYGOIDEI Patterson (1964 : 434)

This suborder contains four monotypic Upper Cretaceous families, probably not closely related. As the caudal skeleton in the type family, the Dinopterygidae, is poorly known, the best known family, the Aipichthyidae, will be described first.

Family AIPICHTHYIDAE Patterson (1964 : 303)

Genus AIPICHTHYS Steindachner (1860 : 763)

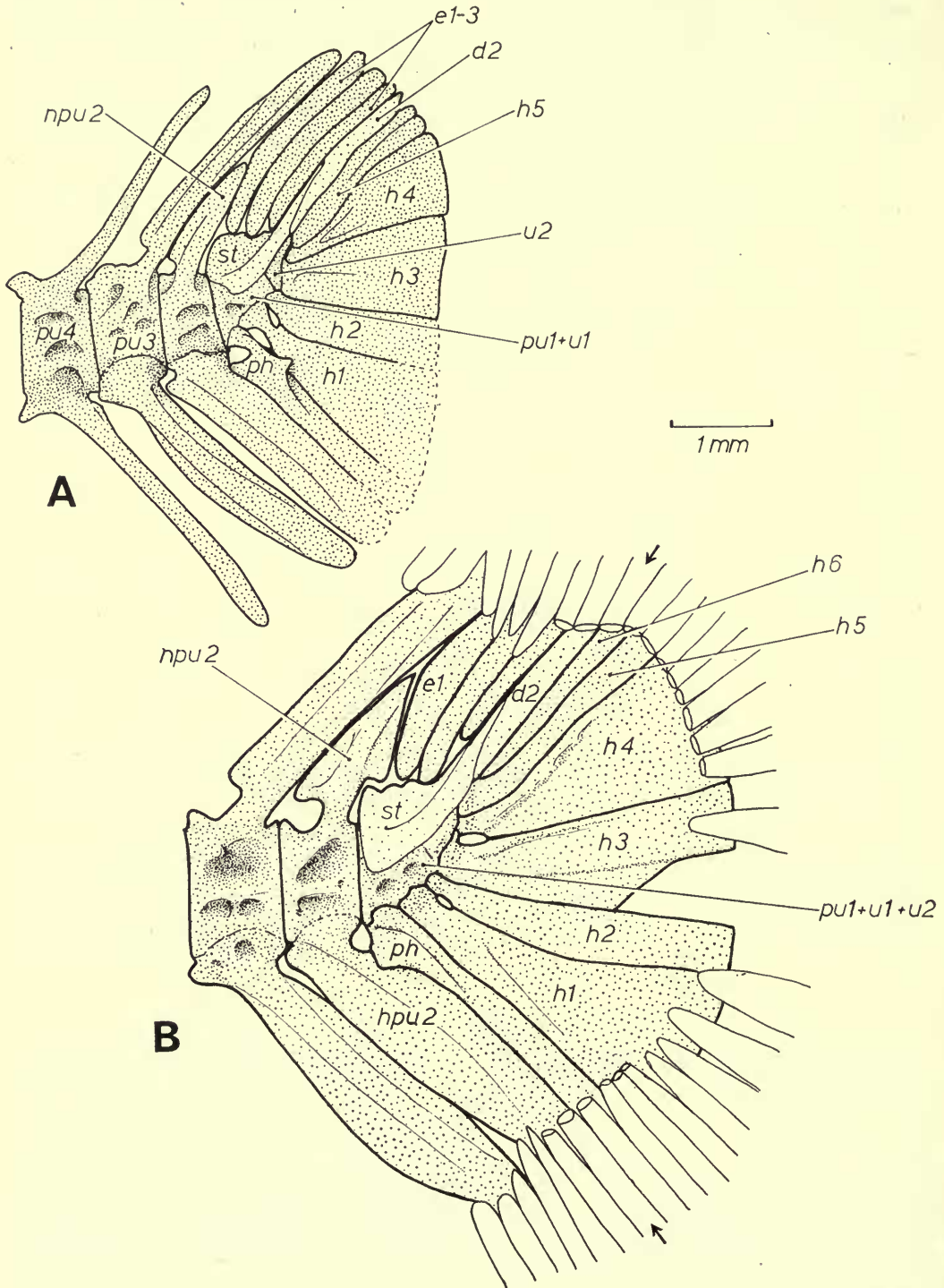
I have seen no material of the type species, *A. pretiosus* Steindachner from the Lower Cenomanian of Dalmatia, and the caudal region is not preserved in *A.*

nuchalis (Dixon) from the English Chalk. The other two species, *A. minor* (Pictet) and *A. velifer* Smith Woodward, both from the Cenomanian of Hakel, Lebanon, are well represented in the British Museum (Natural History). They show a remarkable range of variation in the structure of the caudal skeleton. In most specimens of *Aipichthys* the distal parts of the hypurals, epurals and uroneurals are obscured by the deeply cleft bases of the caudal fin-rays, but in P.82 (*A. minor*, Fig. 11A) the fin-rays are displaced, exposing these bones. In this specimen and in all others the neural and haemal spines of the third pre-ural centrum (pu_3) are broad and elongate and the first procurrent rays of the fin articulate with them. The haemal arches of the second and third pre-ural centra are autogenous. In contrast to all Polymixioidei, the neural spine of the second pre-ural centrum (npu_2) is normally only about half as long as its predecessor, which makes contact with the first epural distally. Though somewhat expanded, this neural spine is more like those of *Elops* (Nybelin 1963, figs. 1, 4) and *Nematonotus* (Fig. 25) than the shorter, broader spine in *Aulolepis* and *Ctenothrissa* (Figs. 2, 4, 5): it does not resemble the very low crest on this centrum in Berycoidei and percoids. In one specimen of *Aipichthys minor*, P.6183 (Fig. 11C), the neural spine of the second pre-ural centrum is fully developed and supports epaxial fin-rays, as in Polymixioidei. This is clearly an individual variation, comparable to those found in certain individuals of *Monocentris* (Fig. 14) and *Siniperca* (Fig. 26), and is recognizable as such by the gap between the spine and the proximal part of the first epural, which is filled by flanges from the posterior face of the spine and from the anterior face of the epural. In all specimens of *Aipichthys* there are three epurals ($eI - 3$) and the first ural and pre-ural centra are fused ($puI + uI$). There is normally a free second ural centrum (u_2 , Figs. 11A, C), but in occasional individuals, like the large specimen shown in Fig. 11B, the second ural centrum is fused into the preceding compound centrum ($puI + uI + u_2$), although the line of fusion is visible in transparency under xylene. There is always a stegural (st) and a second uroneural (d_2). In *A. minor* there are normally six hypurals ($hI - 6$, Figs. 11B, C), as in Polymixioidei, but in P.82 (Fig. 11A) the fifth hypural is partially divided distally suggesting that the sixth is fused into it. In all specimens of *A. velifer* in which the hypurals are visible (P.4743, P.4744, 49486, P.47862) there appear to be only five hypurals. Preceding the principal rays of the caudal fin there are four unsegmented soft rays and three segmented rays in the upper lobe, three unsegmented and three segmented rays in the lower.

Family PHARMACICHTHYIDAE Patterson (1964 : 398)

This family contains only *Pharmacichthys venenifer* Smith Woodward (1942) from the Middle Cenomanian of Hakel, Lebanon. None of the five known specimens of this species has the caudal skeleton sufficiently well preserved to be illustrated, but the holotype, AUB 104691/99, and AUB 101872 show most of the caudal anatomy. The suggestion (Patterson 1964 : 401) that the nearest relative of *Pharmacichthys* is *Aipichthys* is borne out by the structure of the caudal skeleton and fin. In almost every respect the caudal skeleton of *Pharmacichthys* is identical with that of *Aipichthys* (Fig. 11). The foremost caudal fin-rays articulate with the neural and haemal

THE CAUDAL SKELETON IN



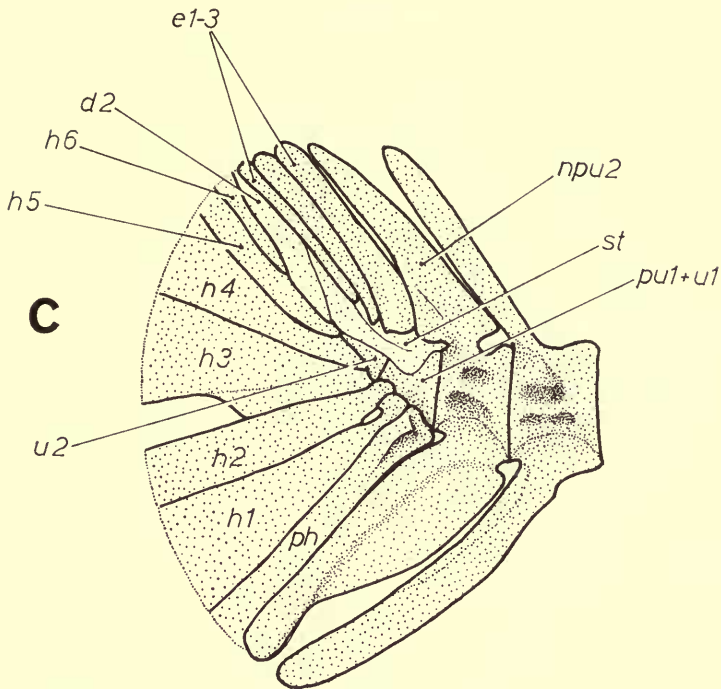


FIG. 11. *Aipichthys minor* (Pictet). Caudal skeleton of **A**, P. 82, standard length 32 mm.; **B**, RSM 1881.5.41, standard length *c.* 50 mm.; **C**, P. 6183, standard length 36 mm. All from Middle Cenomanian, Hakel, Lebanon. For explanation of lettering see p. 102. In **B** arrows mark the outermost (unbranched) principal fin-rays.

spines of the third pre-ural centrum, the neural spine of the second pre-ural centrum is about half as long as its predecessor, as in *Aipichthys*, the haemal spine of the second pre-ural centrum has a broad flange on its anterior edge, there are three epurals and the principal rays of the fin are preceded by four unsegmented soft rays and three segmented rays above, three unsegmented and three segmented rays below. It is impossible to see whether there are five or six hypurals. A further resemblance to *Aipichthys*, not previously noticed, is that the bases of the caudal rays are deeply cleft, overlapping much of the hypurals ("hypurostegy", Le Danois & Le Danois 1964). The only difference from *Aipichthys*, suggested by the holotype, AUB 101872 and AUB 102601, is that the first and second hypurals appear to be fused.

Family **PYCNOSTEROIDIDAE** Patterson (1964 : 389)

The only member of this family is *Pycnosterooides levispinosus* (Hay 1903) from the Middle Cenomanian of Hajula, Lebanon. The caudal skeleton and fin are present in two specimens, P. 13900 (Fig. 12) and AMNH 4519a (Hay 1903, pl. 32, fig. 3). *Pycnosterooides* differs from *Aipichthys* and *Pharmacichthys* in having the foremost rays of the caudal fin inserted on the first epural above and the haemal spine of the third pre-ural centrum below, and in having a fully developed neural spine on

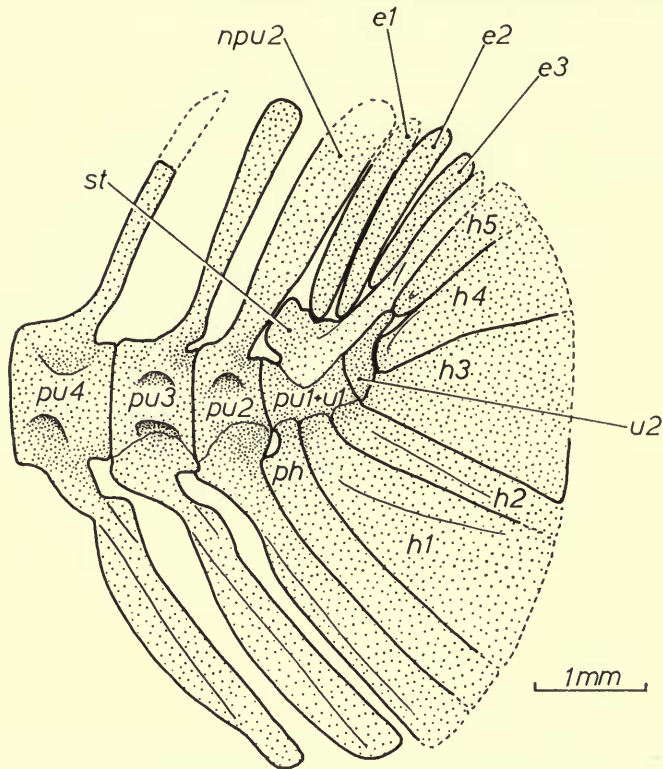


FIG. 12. *Pycnosterooides levispinosus* (Hay). Caudal skeleton of P.13900, standard length *c.* 50 mm., Middle Cenomanian, Hajula, Lebanon. For explanation of lettering see p. 102.

the second pre-ural centrum (*npu2*). This neural spine differs from those of the Polymixioidei in being expanded distally. The haemal arches of the second and third pre-ural centra (*pu2*, *pu3*) are autogenous. In the fusion of the first ural and first pre-ural centra (*pu1 + u1*), the free second ural centrum (*u2*), and the form of the stegural (*st*) and second uroneural (missing in the figured specimen but present in AMNH 4519a) *Pycnosterooides* agrees with *Aipichthys* and the Polymixioidei. There are three epurals (*e1 - 3*). In P.13900, as in *Aipichthys velifer*, there are only five hypurals (*h1 - 5*), but here the first and third are the largest, the third being much larger than the fourth. In AMNH 4519a there are six hypurals. In contrast to *Aipichthys* and *Pharmacichthys* there are only three soft rays, all unsegmented, in front of both the upper and lower principal rays, and the fin-rays are not deeply cleft basally.

Family DINOPTERYGIDAE Jordan (1923 : 173)

This family, the type of the suborder, contains only *Dinopteryx spinosus* (Davis) from the Upper Santonian of Sahel Alma, Lebanon.

The caudal region is very imperfectly preserved in the holotype, 46536/P.4761,

but is more or less completely visible in USNM 22217 and 22219. As in other respects (Patterson 1964 : 392), *Dinopteryx* resembles *Pycnosterooides* in the caudal skeleton. The second pre-ural centrum has a fully developed neural spine and both this and the preceding neural spine are expanded distally, as in *Pycnosterooides* (Fig. 12). As in *Pycnosterooides* there are three epurals, the first ural and pre-ural centra are fused, there is a free second ural centrum, a stegural and a second uroneural. USNM 22219 shows that there were at least three upper hypurals, shaped as in *Pycnosterooides*, but it is impossible to be certain whether or not a small sixth hypural was present. The foremost procurent caudal rays articulate with the neural spine of the second pre-ural centrum above and the haemal spine of the third pre-ural centrum below, further forwards than in *Pycnosterooides*. There are four spines and two segmented rays in front of the principal rays above, three spines and two segmented rays below, both the holotype and USNM 22217 showing that the foremost procurent rays were true spines, a difference from other *Dinopterygoidei*.

Suborder BERYCOIDEI Patterson (1964 : 433)

This suborder, containing eight living families, is represented in the Cretaceous only by two families, the Trachichthyidae and Holocentridae. A detailed discussion of the relationships between these two families in the Cretaceous will be found in

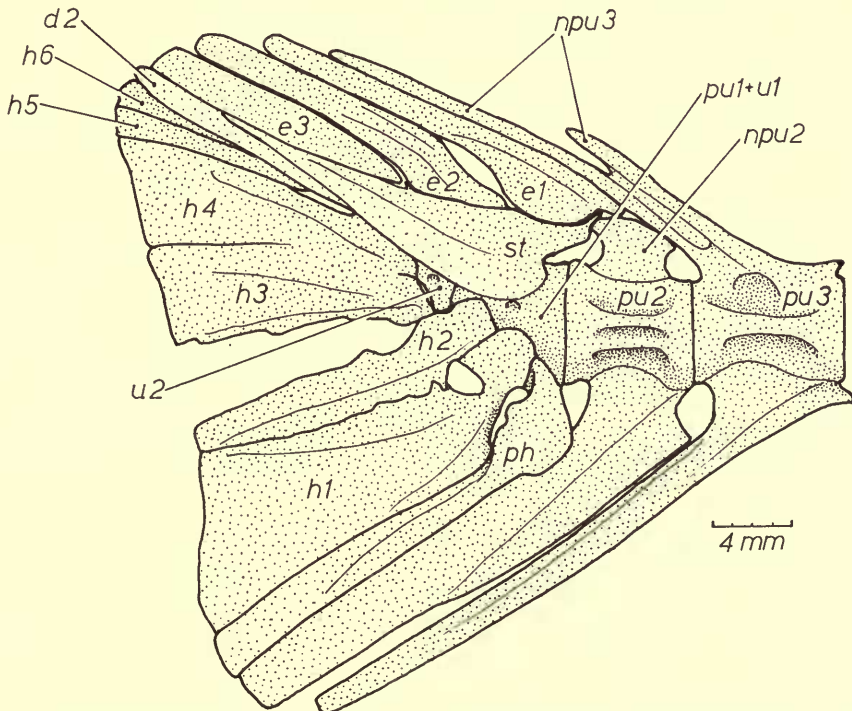


FIG. 13. *Hoplostethus mediterraneus* Cuvier & Valenciennes. Caudal skeleton of a dried skeleton, 1878.4.5.8, standard length 190 mm., Japan. For explanation of lettering see p. 102.

Patterson (1967). Among living Berycoidei, the caudal skeleton of *Centroberyx affinis* (Berycidae) has been illustrated by Regan (1911, fig. 2), those of *Hoplostethus* (Trachichthyidae), *Holocentrus* and *Myripristis* (both Holocentridae) are briefly discussed by Gosline (1961: 14) and a caudal skeleton of *Holocentrus ascensionis* is figured by Rosen (1964, fig. 23D). Fig. 13 shows the caudal skeleton of the living *Hoplostethus mediterraneus* (Trachichthyidae). In most respects this is typical of primitive Berycoidei, with autogenous haemal spines on the second and third pre-ural centra, the second pre-ural centrum without a neural spine, bearing only a low, broad crest (*npu2*) which lies below the proximal end of the first epural, three epurals (*ei - 3*), six hypurals (*hi - 6*), a free second ural centrum (*u2*), a stegural (*st*) and a second uroneural (*dz*). In the specimen illustrated the neural spine of the third pre-ural centrum (*npu3*) is double distally and the third and fourth hypurals are fused proximally: these features are individual abnormalities. The neural crest on the second pre-ural centrum is autogenous—this is a primitive feature which also occurs in primitive myctophoids (*Nematonotus* and *Aulopus*, p. 81). In *Hoplostethus* the foremost procurrent fin-rays articulate with the neural and haemal spines of the third pre-ural centrum. In living trachichthyids (*Hoplostethus*, *Trachichthys*, *Paratrachichthys*, *Gephyroberyx*) the nineteen principal caudal rays are normally preceded by six spines and one segmented ray above and below.

The caudal skeleton in living holocentrids is described below (p. 75, Fig. 20). In Berycidae (Regan 1911, fig. 2) the caudal skeleton is advanced over the trachichthyid condition in having both the second ural centrum and the stegural fused into the compound first ural and pre-ural centrum. Nothing is known of the caudal skeleton in Korsogasteridae and Anomalopidae. Dissection of single specimens of *Diretmus* (Diretmidae) and *Anoplogaster* (Anoplogasteridae) shows that both resemble Berycidae in having the stegural and second ural centrum fused into the preceding compound centrum, while in *Anoplogaster* the second uroneural is lost and in *Diretmus* the sixth hypural is lost and there is fusion between the first and second hypurals and between the third and fourth hypurals. In the Stephanoberycoidei, which appear to be only specialized derivatives of the Berycoidei, *Gibberichthys* (Gibberichthyidae) agrees with trachichthyids such as *Hoplostethus* in the caudal skeleton but *Melamphaes* (Melamphaeidae) has both the stegural and second ural centrum fused with the preceding centrum, a much reduced second uroneural, only five hypurals and fusion within the upper and lower hypurals. All living berycoids and stephanoberycoidei seem to be characterized by the presence of spinous procurrent caudal rays.

In *Monocentris* (Monocentridae) the caudal skeleton normally shows the same major features as the figured specimen of *Hoplostethus* (even to the partial doubling of the neural spine of the third pre-ural centrum), but in one of the available skeletons (Fig. 14) there is a fully developed neural spine on the second pre-ural centrum (*npu2*) and the neural spine of the third pre-ural centrum is single. There are three epurals (*ei-3*), so that in this individual the neural spine on the second pre-ural centrum has apparently developed instead of the normal doubling of the neural spine of the preceding centrum. The caudal skeleton of this specimen resembles those of polymixioids and the dinopterygoids *Pycnosterooides* and *Dinopteryx*, but

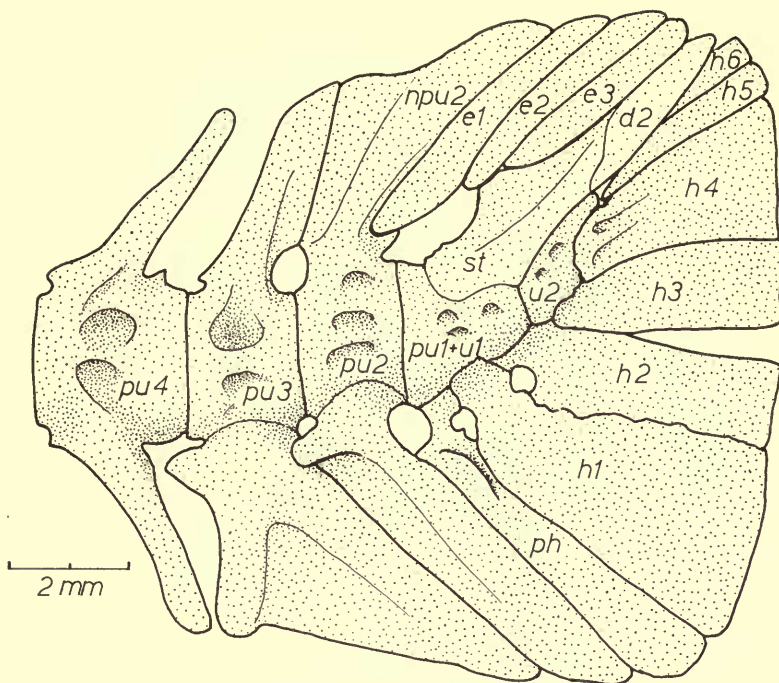


FIG. 14. *Monocentris japonicus* (Houttuyn). Caudal skeleton of a dried skeleton showing a neural spine on the second pre-ural centrum, 1862.11.1.47, standard length 125 mm., Japan. For explanation of lettering see p. 102.

it is questionable whether this is significant. However, *Monocentris* seems to be the only living berycoid in which the procurrent caudal rays are sometimes not spines but unsegmented soft rays: of four specimens examined, one has no spines and one has only one spine in front of the lower caudal lobe and none above. *Monocentris* is a fish of highly specialized appearance and the skull suggests that the Monocentridae are derivatives of the Trachichthyidae, but there is a patch of teeth on the endopterygoid (Starks 1904 : 618), a character otherwise unknown in Berycoidei, and this and the occasional absence of procurrent caudal spines suggest that the Monocentridae may have had a long independent history.

Family TRACHICHTHYIDAE Bleeker (1859)

The caudal skeleton of the living *Hoplostethus mediterraneus* is described above (Fig. 13).

Genus *HOPLOPTERYX* Agassiz (1838 : 4)

Hoplopteryx, with eight species ranging from the Middle Cenomanian to the Upper Senonian, is the longest-ranging and largest genus of Cretaceous Trachichthyidae.

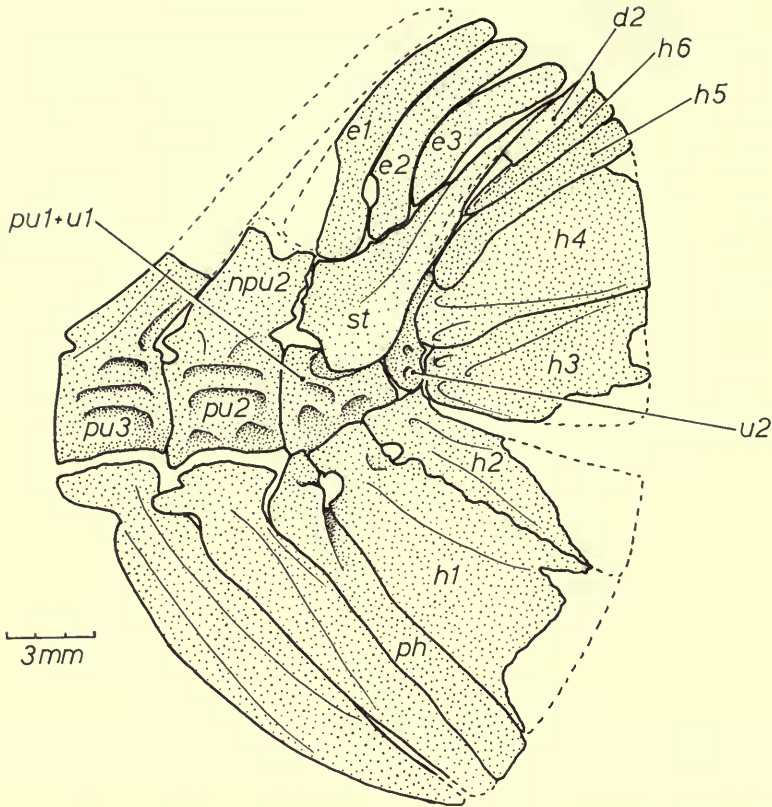


FIG. 15. *Hoplopteryx lewesiensis* (Mantell). Caudal skeleton of P. 1948b, standard length c. 175 mm., Chalk, Sussex. For explanation of lettering see p. 102.

In the type species, *H. antiquus* Agassiz from the Campanian of Westphalia, I have seen no specimens in which the caudal skeleton is preserved. The best known species is *H. lewesiensis* (Mantell) which ranges throughout the English Chalk: several specimens show the caudal skeleton (Figs 15, 16) which is almost identical with that of the living *Hoplostethus* (Fig. 13), with the neural arch of the second pre-ural centrum (*npu2*) reduced (though not so much as in *Hoplostethus*), the haemal arches of the second and third pre-ural centra autogenous, three epurals (*e1-3*) of which the first is especially large, a stegural (*st*) and a second uroneural (*d2*), a free second ural centrum (*u2*) and six hypurals (*h1-6*), the uppermost very small. The neural arch of the second pre-ural centrum is not autogenous as it is in *Hoplostethus*. The foremost caudal fin-rays are inserted on the first epural above and on the haemal spine of the third pre-ural centrum below. There are only three spines and one segmented ray in front of the upper principal rays and two spines and one segmented ray in front of the lower.

The other species of *Hoplopteryx* in the English Chalk are *H. simus* Smith Woodward, *H. macracanthus* Patterson and *H. gephyrognathus* Patterson. The caudal

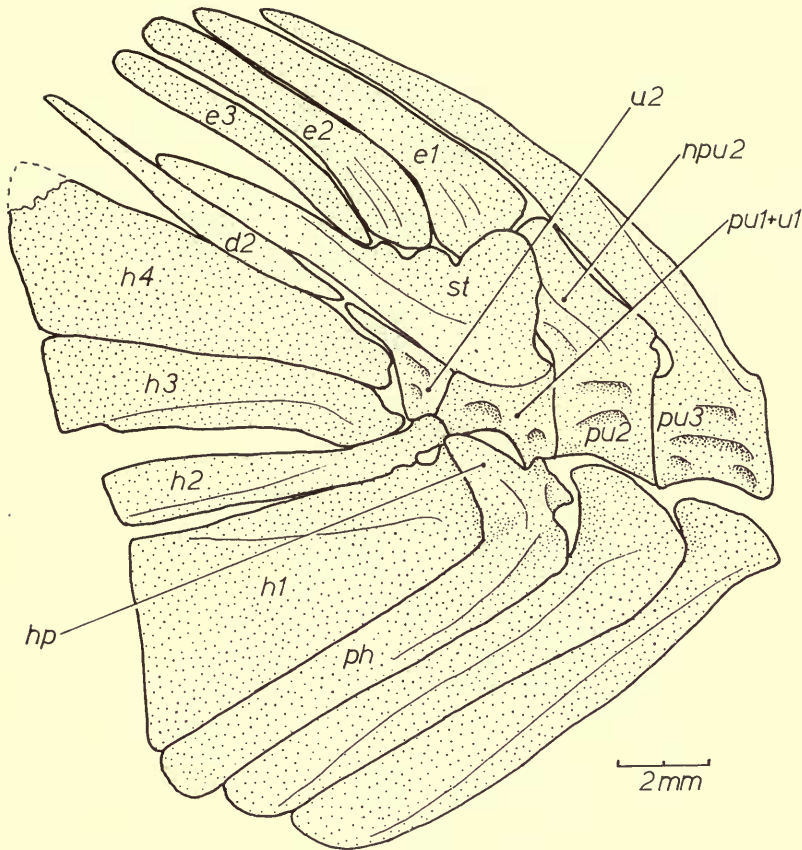


FIG. 16. *Hoplopteryx lewesiensis* (Mantell). Caudal skeleton of P. 5421, standard length c. 135 mm., Lower Chalk, Lewes, Sussex. For explanation of lettering see p. 102. The second uroneural is displaced ventrally and the fifth and sixth hypurals are missing.

skeleton of *H. simus* is exposed in P. 11202, that of *H. macracanthus* in P. 30186: neither appears to differ from *H. lewesiensis* in any way. The caudal region is not preserved in the two known specimens of *H. gephyrognathus*.

The earliest species of *Hoplopteryx* is *H. lewisi* (Davis) from the Middle Cenomanian of Hakel, Lebanon. In this species the caudal skeleton and fin are exposed in P. 10709 and partially shown in the holotype, P. 4758. *H. lewisi* seems to agree with *H. lewesiensis* in every detail, even to the insertion of the foremost upper fin rays on the first epural, except that there are four spines and one segmented ray in front of the upper principal rays, three spines and one segmented ray in front of the lower.

The remaining two species of *Hoplopteryx*, *H. syriacus* (Pictet & Humbert) and *H. spinulosus* Smith Woodward, are from the Upper Santonian of Sahel Alma, Lebanon. In *H. spinulosus* I have seen no specimen in which the caudal skeleton

is preserved. In *H. syriacus* parts of the caudal skeleton are preserved in 49553 and they show nothing to distinguish the species from *H. lewesiensis*.

Genus *LISSOBERYX* Patterson (1967 : 73)

The type species, *L. dayi* (Smith Woodward 1942), is from the M. Cenomanian of Hakel and Hajula, Lebanon. I have briefly described the caudal skeleton (Patterson 1967 : 78) which is preserved in AUB 108926 (Fig. 17) and AUB 101997. The caudal skeleton agrees well with those of *Hoplostethus* (Fig. 13) and *Hoplopteryx* (Figs 15, 16). The neural spine of the second pre-ural centrum (*npu2*) is reduced to about the same extent as in *Hoplopteryx*, there are three epurals (*e1-3*), the

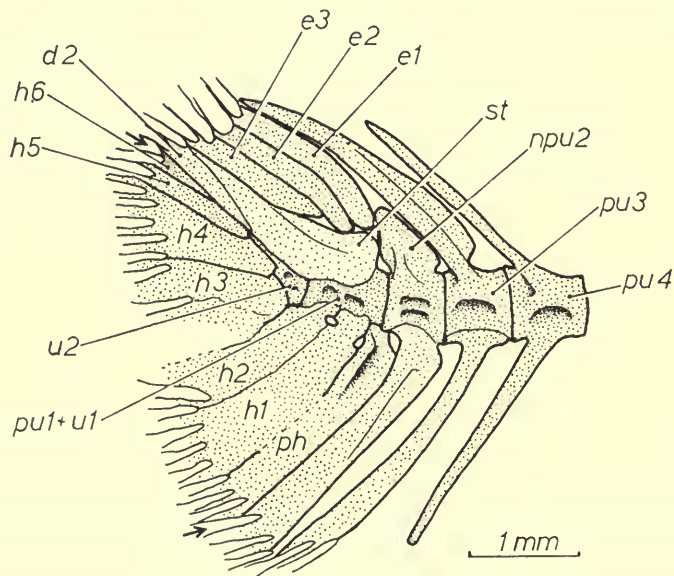


FIG. 17. *Lissoberyx dayi* (Smith Woodward). Caudal skeleton of AUB 108926, standard length 34 mm., Middle Cenomanian, Hajula, Lebanon. For explanation of lettering see p. 102. Arrows mark the outermost (unbranched) principal fin-rays.

first long and closely applied distally to the neural spine of the third pre-ural centrum, a stegural (*st*) and a second uroneural (*d2*), and six hypurals (*h1-6*). The only significant differences from *Hoplopteryx* and *Hoplostethus* are that the fused first ural and pre-ural centrum is longer, with clear signs in the surface sculpture of its origin from two centra, and that the second ural centrum is also longer, so that the caudal skeleton appears more upturned. As in *Hoplopteryx* the foremost caudal rays articulate with the first epural above and the haemal spine of the third pre-ural centrum below. The principal rays are preceded by four spines and one unsegmented ray above, three spines and one segmented ray below.

Genus *ACROGASTER* Agassiz (1838 : 5)

I have seen no specimens of *A. parvus* Agassiz, the type species, or of *A. brevicostatus* von der Marck, both these species from the Campanian of Westphalia being poorly known. The remaining species, *A. heckeli* (Pictet) and *A. daviesi* (Davis), from the Upper Santonian of Sahel Alma, Lebanon, are common and several specimens in the British Museum (Natural History) show the caudal skeleton clearly: I can find no differences between these two species in caudal anatomy. A specimen of

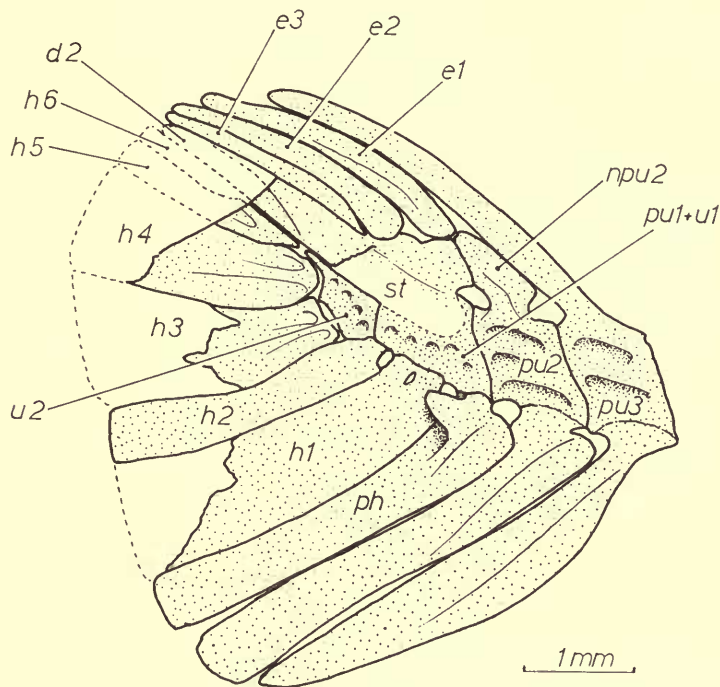


FIG. 18. *Acrogaster heckeli* (Pictet). Caudal skeleton of P. 4155, standard length *c.* 55 mm., Upper Santonian, Sahel Alma, Lebanon. For explanation of lettering see p. 102.

A. heckeli is illustrated in Fig. 18. As in the other trachichthyids described above, the neural spine of the second pre-ural centrum is reduced (*npu2*), there are three epurals (*e1-3*), a stegural (*st*), a second uroneural (*d2*) and six hypurals (*h1-6*). The fused first ural and pre-ural centra (*pu1 + u1*) and the second ural centrum (*u2*) are elongate, as in *Lissoberyx*, and the caudal skeleton appears strongly upturned. As in *Hoplopteryx* and *Lissoberyx*, the foremost caudal rays articulate with the first epural above and the haemal spine of the third pre-ural centrum below. The principal caudal rays are preceded by four or five spines and one segmented ray above, three or four spines and one segmented ray below.

Genus *TUBANTIA* Patterson (1964 : 413)

The only species is *T. cataphractus* (von der Marck), from the Campanian of Westphalia, in which the caudal skeleton is well exposed in P.21984 (Fig. 19). *Tubantia* agrees with other trachichthyids in the reduction of the neural spine of the second pre-ural centrum (*npu2*), the three epurals (*e1-3*), stegural (*st*), second uro-

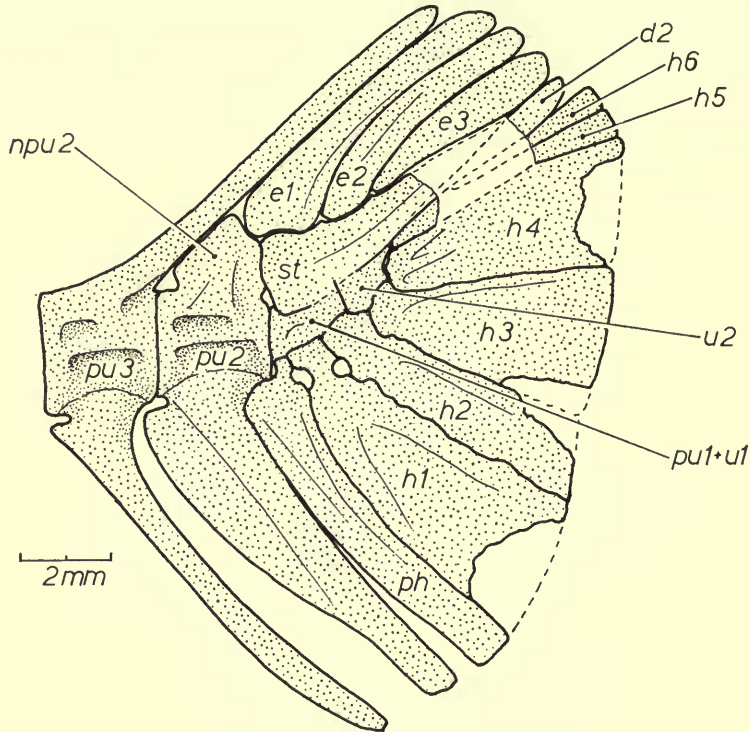


FIG. 19. *Tubantia cataphractus* (von der Marck). Caudal skeleton of P.21984, standard length 130 mm., Campanian, Baumberg, Westphalia. For explanation of lettering see p. 102.

neural (*d2*), and six hypurals (*h1-6*). As in *Hoplostethus*, the fused first ural and pre-ural centrum (*pu1 + u1*) is only as long as the preceding centrum. *Tubantia* differs from other Cretaceous trachichthyids and resembles living forms in having the number of procurent rays increased to nine spines and two segmented rays above, six spines and two segmented rays below, these small rays extending forwards in front of the tips of the neural and haemal spines of the third pre-ural centrum.

Genus *GNATHOBERYX* Patterson (1967 : 81)

The type and only species, *G. stigmatosus* Patterson (1967 : 82), from the Upper Santonian of Sahel Alma, Lebanon, is known by two specimens and the caudal skeleton is preserved only in the holotype, AUB 100402, where it is compressed and

distorted. So far as can be seen, the caudal skeleton and fin agree with other Cretaceous trachichthyids such as *Lissoberyx*, *Hoplopteryx* and *Acrogaster*, with the neural spine of the second pre-ural centrum reduced, the stegural free, a free second ural centrum, and the upper principal rays preceded by four spines and one segmented ray, the foremost articulating with the first epural.

Family **HOLOCENTRIDAE** Richardson (1846)

The caudal skeleton of the living *Myripristis adustus* is shown in Fig. 20: it shows no significant differences from those of several species of *Holocentrus*. The neural and haemal spines of the fourth (pu_4) and fifth pre-ural centra are expanded but short. The neural spine of the second pre-ural centrum (npu_2) is greatly reduced

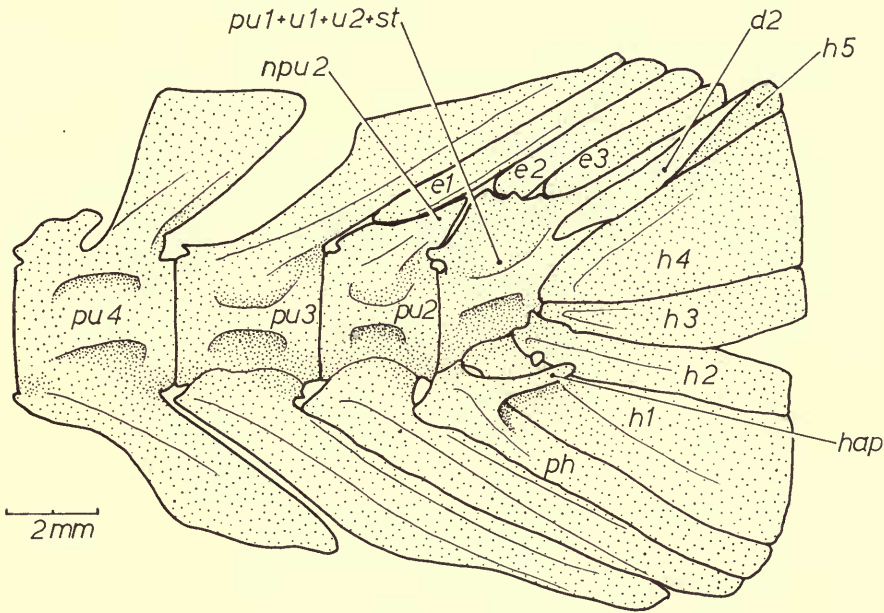


FIG. 20. *Myripristis adustus* Bleeker. Caudal skeleton of a dried skeleton, 1858.4.21.239, standard length 155 mm., Amboina. *hap*, hypurapophysis; for explanation of other lettering see p. 102.

(and not autogenous as it is in *Hoplostethus*), with the tip of the first epural lying above it. The haemal arches of the second and third pre-ural centra (pu_2 , pu_3) are autogenous and there are three epurals (e_1-3). In contrast to the trachichthyids the two ural centra, the first pre-ural centrum and the stegural are all fused into a single structure ($pu_1 + u_1 + u_2 + st$) and there are only five hypurals (h_1-5) the uppermost hypural present in trachichthyids having been lost. The second uroneural (d_2) is free and fits proximally into a notch in the stegural rather than lying below and behind it. In *Myripristis* the foremost caudal rays articulate with the first epural above (as in most Cretaceous trachichthyids) and with the haemal

spine of the third pre-ural centrum below. In *Holocentrus* the foremost rays articulate with the neural and haemal spine of the third pre-ural centrum. In *Myripristis* the principal caudal rays are preceded by four spines and one segmented ray above and below. Rosen (1964, fig. 23D) has figured a caudal skeleton of *Holocentrus ascensionis* which differs from all the Recent holocentrid skeletons that I have seen in having a free second ural centrum. Rosen does not say how large his specimen was, but if it was an alizarin-stained juvenile this difference can be explained.

Genus **CAPROBERYX** Regan (1911 : 8)

In the type species, *C. superbus* (Dixon) from the Turonian of the English Chalk, the caudal skeleton is exposed in P. 3979 (Fig. 21). The neural and haemal spines of the fourth (*pu4*) and fifth pre-ural centra are normal, not expanded as in living holocentrids. The haemal arches of the second and third pre-ural centra (*pu2*, *pu3*) are autogenous, the neural spine of the second pre-ural centrum (*npu2*) is reduced and there are three epurals (*e1-3*), all as in living holocentrids. In contrast to living holocentrids, the stegural (*st*) is not fused to the underlying centrum (*pu1 + u1*) and the second ural centrum (*u2*) is free. The second uroneural (*d2*) is fused to the stegural (*st*) distally, but this is perhaps only a consequence of the very large size (standard length *c.* 40 cm) of this specimen. As in living holocentrids there are only five hypurals, but the distribution of the branched principal fin-rays (one on

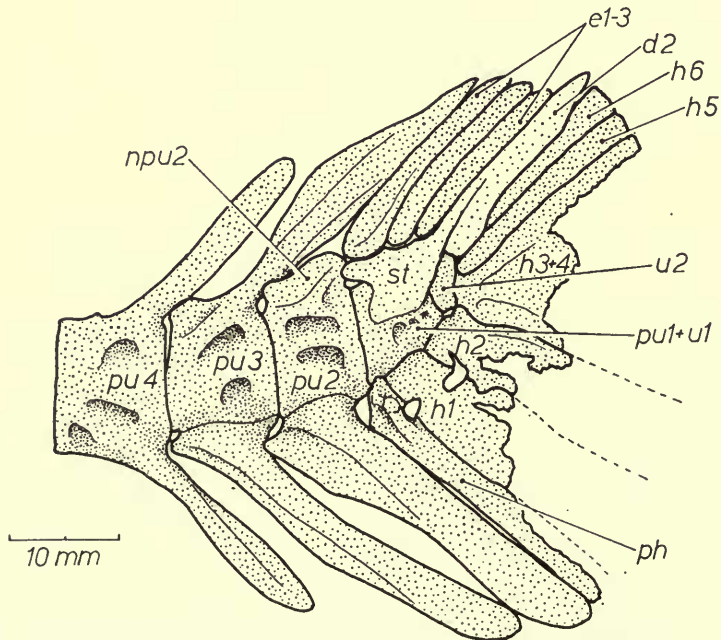


FIG. 21. *Caproberyx superbus* (Dixon). Caudal skeleton of P. 3979, standard length *c.* 400 mm., Chalk, Sussex. For explanation of lettering see p. 102.

the uppermost hypural, two on the one below and six on the next) shows that the three upper hypurals are the third and fourth fused ($h_3 + 4$), the fifth (h_5) and the sixth (h_6), for in living holocentrids the three upper hypurals, the third, fourth and fifth, bear two, six and one branched principal rays respectively. *Caproberyx* therefore agrees with the trachichthyids in retaining the small sixth hypural, and the fusion of the third and fourth hypurals shown by P.3979 is again probably merely a consequence of the large size of the fish. As in *Myripristis* and most Cretaceous trachichthyids, the foremost caudal fin-rays articulate with the first epural above and the haemal spine of the third pre-ural centrum below, and there are probably four spines and one segmented ray in front of the principal caudal rays above and below. Characters of the skull and fins suggest that *Caproberyx* is the most primitive holocentrid known, lying near to the common stock of the Holocentridae and Trachichthyidae (Patterson 1964 : 359; 1967 : 103). This is confirmed by the structure of the caudal skeleton in *C. superbus*, for in the six hypurals, the free stegural and second ural centrum, and the unexpanded neural and haemal spines of the posterior caudal vertebrae, this species resembles the trachichthyids rather than other holocentrids.

The other species of *Caproberyx* are *C. polydesmus* (Arambourg 1954) from the Lower Cenomanian of Jebel Tselfat, Morocco, and *C. pharsus* Patterson (1967 : 97) from the Middle Cenomanian of Hakel, Lebanon. *C. pharsus* is known only by a specimen lacking the caudal region. *C. polydesmus* is known only by the holotype: Arambourg's figure (1954, pl. 19, fig. 1) shows that the neural and haemal spines of the fourth and fifth pre-ural centra are not expanded, as in *C. superbus*, and he described the principal rays as having five or six small rays in front of them in each lobe.

Genus *STICHOCENTRUS* Patterson (1967 : 88)

The type and only species is *S. liratus* Patterson from the Middle Cenomanian of Hajula, Lebanon. The caudal skeleton is well preserved in AUB 108923 (Fig. 22) and is partially shown in AUB 108927 and 108929. The neural and haemal spines of the fifth pre-ural centrum are unmodified but those of the fourth (pu_4) are expanded, though not so strongly as in living holocentrids. The autogenous haemal arches on the second and third pre-ural centra, the reduced neural spine on the second pre-ural centrum (npu_2) and the three epurals ($eI-3$) are as in *Caproberyx* and living holocentrids. The stegural is fused with the underlying centrum ($pu_1 + u_1 + u_2 + st$) anteriorly. The second uroneural (d_2) is free and lies below and behind the first, not notched into the first as it is in living holocentrids. The second ural centrum is fused to the compound first pre-ural and ural centrum in AUB 108923 (standard length *c.* 75 mm.) although the line of fusion is clearly seen, but in AUB 108929, a much smaller specimen (standard length *c.* 35 mm.) the centrum appears free. As in living holocentrids, there are only five hypurals ($hI-5$), the small sixth hypural present in *Caproberyx* having been lost. As in *Myripristis*, the foremost caudal rays are inserted on the first epural above and the haemal spine of the third pre-ural centrum below, and there are four spines and one segmented ray in front of both the upper and lower principal rays.

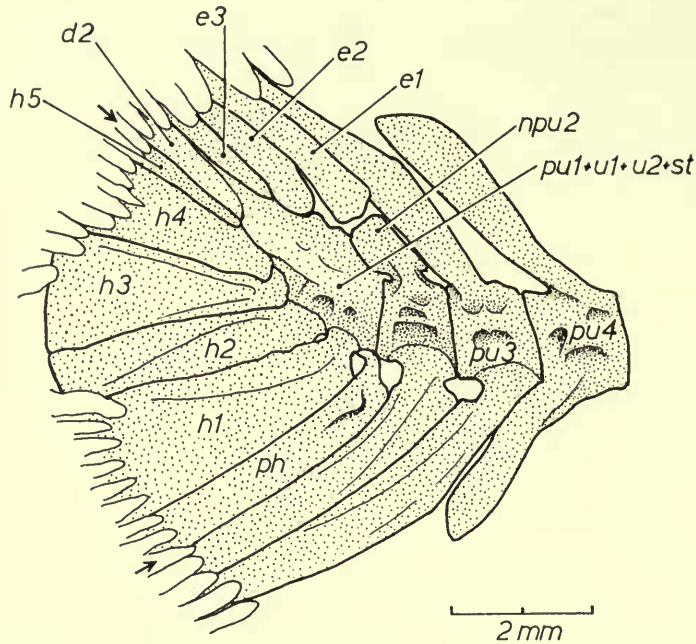


FIG. 22. *Stichocentrus livatus* Patterson. Caudal skeleton of AUB 108923, standard length *c.* 75 mm., Middle Cenomanian, Hajula, Lebanon. For explanation of lettering see p. 102. Arrows mark the outermost (unbranched) principal fin-rays.

As in the skull and fins, *Stichocentrus* is more advanced towards the living holocentrids than *Caproberyx* in the expanded neural and haemal spines of the fourth pre-ural centrum, the five hypurals and the partial fusion of the stegural and second ural centrum with the preceding centrum.

The remaining Cretaceous holocentrids are *Trachichthyooides ornatus* Smith Woodward (1902), known only by an isolated head from the English Chalk, and *Kansius sternbergi* Hussakof (1929) known by the two syntypes from the Niobrara Formation, Gove Co., Kansas. Nothing is known of the caudal anatomy of these forms.

Order LAMPRIDIFORMES

Suborder LAMPRIDOIDEI Berg (1940 : 463)

This suborder is used to contain both the Lampridoidei (*Lampris* only) and the Veliferoidei (*Velifer*, etc.) of Berg (Bonde 1966).

? Family VELIFERIDAE Bleeker (1860)

Genus *BATHYSOMA* Davis (1890 : 424)

The type and only species is *B. lutkeni* Davis from the Danian stage of southern Sweden. The caudal skeleton is partially preserved in two specimens in the British Museum (Natural History). P. 9947 (Fig. 23A) shows that the upper hypurals are

fused into a triangular plate and that this plate is fused basally with the second ural centrum ($u_2 + uh$). Above the second pre-ural centrum (pu_2) and the fused first pre-ural and ural centra ($pu_1 + u_1$) there are two elongate bones: the second of these (e) is certainly an epural but it is impossible to be certain whether the first is an epural or the neural arch and spine of the second pre-ural centrum. Above the upper hypural plate there is a third slender bone of uncertain nature. P.9948

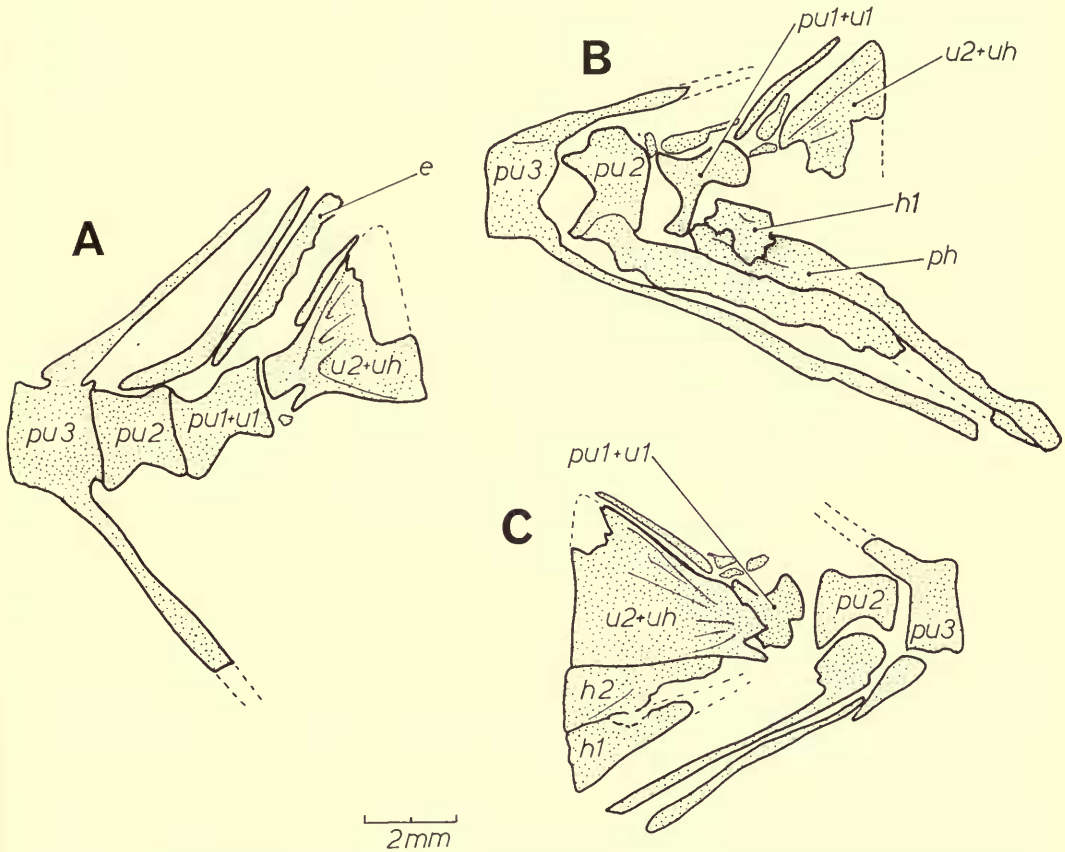


FIG. 23. *Bathysoma lutkeni* Davis. Caudal skeleton of **A**, P.9947, standard length *c.* 95 mm.; **B**, **C**, P.9948 (part and counterpart), standard length 78 mm. Both from Danian, Limhamn, southern Sweden. $u_2 + uh$, second ural centrum fused with one or more upper hypurals; for explanation of other lettering see p. 102.

(in counterpart, part and counterpart shown in Fig. 23B, C) shows the second pre-ural centrum (pu_2) with an autogenous haemal arch and no sign of a neural spine, the fused first pre-ural and ural centra ($pu_1 + u_1$) bearing the parhypural (ph) and the first hypural (h_1), the distal part of the second hypural (h_2), and the upper hypural plate with a fragment of the second ural centrum fused to it ($u_2 + uh$). As in P.9947, there is a slender bone lying above the upper hypural plate. The bones above the first and second pre-ural centra are shattered and displaced. Although

these two specimens are far from complete, they show that in *Bathysoma* the haemal arch of the second pre-ural centrum was autogenous, the first pre-ural and ural centra were fused, the parhypural and the first and second hypurals were separate and autogenous, there was at least one epural, and the upper hypurals were fused with each other and with the second ural centrum. On the available material it is difficult to interpret the upper hypural plate and the slender bone above it, which may be an epural, a stegural or a free hypural. In the upper hypural plate at least three hypurals can be recognized in transparency under xylene, presumably hypurals 3-5, but the uppermost part of the plate is of a different texture, suggesting that the stegural may also be fused into the structure, a most unusual condition which can only be confirmed on more complete material.

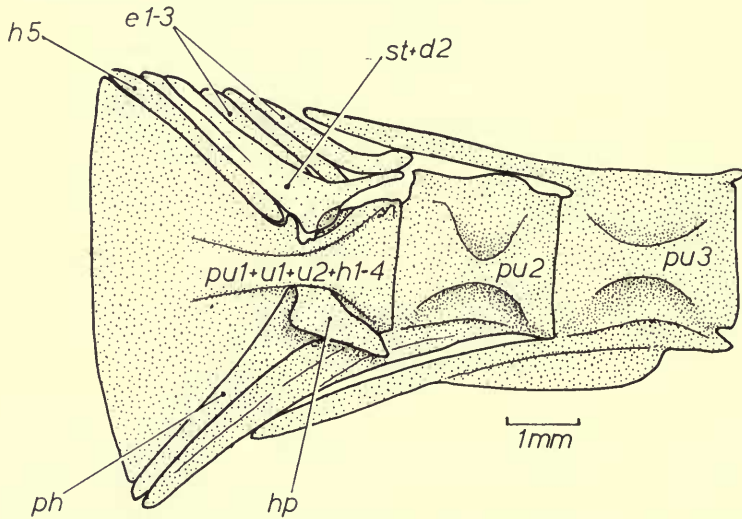


FIG. 24. *Mene maculata* (Bloch & Schneider). Caudal skeleton of a dried skeleton, 1866.6.8.59, standard length 95 mm., Taiwan. *hp*, hypurapophysis; for explanation of other lettering see p. 102.

The caudal skeleton of *Bathysoma* is very different from that of *Mene*, the only genus of the Menidae, in which *Bathysoma* was previously placed (Patterson 1964: 423). In the living *Mene maculata* (Fig. 24) the first pre-ural centrum, both the ural centra, and all but the uppermost hypural are fused into a symmetrical, fan-shaped plate ($pu1 + u1 + u2 + h1-4$). The parhypural (*ph*) has a very large hypurapophysis (*hp*) and lies free below this plate. The uppermost hypural (*h5*) is also free, articulating with a hook on the upper edge of the hypural plate. There are three normal epurals (*e1-3*) and the neural arch of the second pre-ural centrum (*pu2*) is reduced to a very low crest. The stegural (*st + d2*) is autogenous, articulating with the underlying compound centrum by a large and clearly mobile joint. The distal part of the shaft of the stegural is grooved longitudinally in *M. maculata*; in the Middle Eocene species *M. rhombus* (Volta) and *M. oblongus* (Agassiz), in which the caudal skeleton is otherwise identical with that of the living species, there

is a free second uroneural, and the groove on the shaft of the stegural in *M. maculata* clearly marks the line of fusion between the first and second uroneurals. *Mene* has seventeen principal caudal rays with fifteen branched, the outermost two or three rays unsegmented and the inner ones only sparsely segmented, preceded by five unsegmented but divided (in the median plane) rays above and four below. The bases of the caudal rays are deeply cleft, covering much of the hypural plate. The caudal skeleton of *Mene* can be derived from the basal perciform type (p. 87) by fusion of the first four hypurals with each other and with the supporting centra, and the caudal fin has the perciform number of rays. The caudal skeleton of *Bathysoma* is of a much more primitive type, differing from that of Beryciformes mainly in the fusion of the upper hypurals with the second ural centrum. A caudal skeleton of this type occurs in the Lampridiformes *Velifer* (Gosline 1961; fig. 3D), *Palaeocentrotus* (Kühne 1941, fig. 2; Bonde 1966) and *Lampris*, and the known skeletal features of *Bathysoma* (Patterson 1964, fig. 90) agree as well with *Palaeocentrotus* and *Velifer* (Regan 1907; Smith 1951) as they do with *Mene*. The holotype of *Bathysoma lutkeni*, in Copenhagen, shows that the supraoccipital crest is attached to the skull roof only at the posterior end, with a gap between it and the frontal crest (Bonde, personal commn): an exactly similar supraoccipital crest occurs in Bonde's (1966) ? veliferid from the Lower Eocene [Mo-clay], while in *Palaeocentrotus* there is a large foramen between the supraoccipital and frontal crests (Kühne 1941, fig. 3). Provisionally *Bathysoma* may be placed in the Veliferidae but, like Bonde's Eocene form, it may well prove to be closer to *Palaeocentrotus*.

Order SALMONIFORMES (Greenwood *et al.* 1966)

Suborder MYCTOPHOIDEI

The most generalized of living myctophoids is *Aulopus* (Aulopodidae, Regan 1911a : 121). The caudal skeleton of *Aulopus* is briefly discussed by Gosline (1961 : 10), who notes that this genus is one of the few living teleosts retaining large caudal scutes in front of the caudal lobes. The caudal skeletons of more advanced myctophoids have been figured by Hollister (*Synodus*, *Trachinocephalus*, 1937a, figs 1-14), Gosline (*Chlorophthalmus*, 1961, fig. 2B), Rosen (*Myctophum*, 1964, fig. 23C) Greenwood *et al.* (*Neoscopeus*, 1966, fig. 3C) and Weitzman (*Parasudis* and *Saurida* 1967, figs 17, 18). In *Aulopus* the caudal skeleton is almost identical with that of the Cretaceous *Ctenothrissa* (Figs 4, 5), with a free second ural centrum, a stegural and a second uroneural, three epurals and six hypurals, of which the first and third are the largest. The only differences from *Ctenothrissa* are that the haemal arch of the third pre-ural centrum and the neural arch of the second pre-ural centrum are autogenous, the neural spine of the second pre-ural centrum is less expanded, more spine-like, and just over half as long as its predecessor, and the second ural centrum has a long posterior process. In all these characters, *Aulopus* appears to be more primitive than *Ctenothrissa*. In other living myctophoid families conditions are much as in *Aulopus*, but the caudal scutes are lost, the neural spine of the second pre-ural centrum ceases to be autogenous and becomes shorter and expanded, the first epural tending to move forwards above it, there is often fusion within the upper

and lower hypurals, the sixth hypural and one epural may be lost (Synodontidae), and the second ural centrum and stegural may fuse with the compound first ural and pre-ural centrum. These trends are very like those seen within the Berycoidei (p. 68; cf. figs. 23C, D in Rosen 1964).

In the Upper Cretaceous myctophoids were abundant, the best known genera being *Sardinioides*, *Acrognathus*, *Cassandra* (= *Leptosomus*) and *Nematonotus*. *Nematonotus* appears to be the most primitive of these and will serve as an example. Figure 25 shows specimens of *Nematonotus bottae* (Pictet & Humbert), from the Cenomanian of Hakel, Lebanon, and *N. longispinus* (Davis), from the Cenomanian

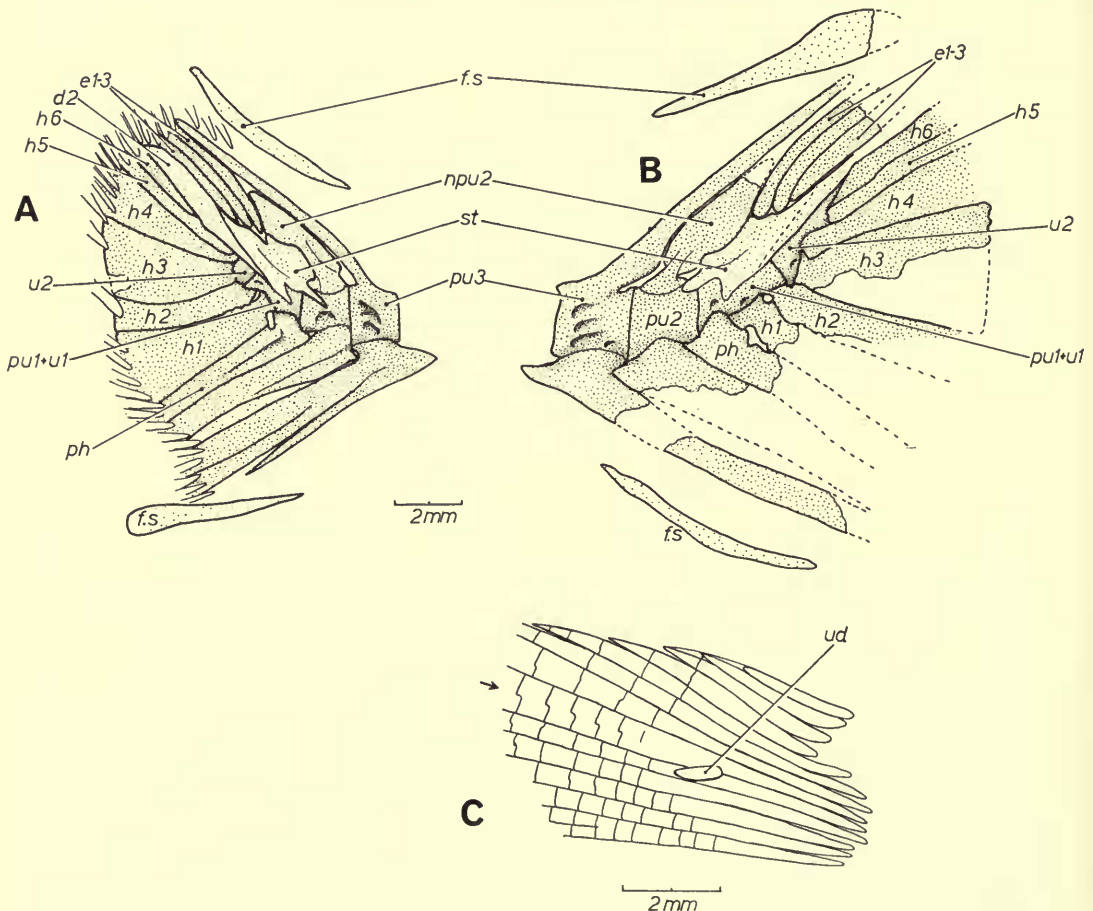


FIG. 25. The caudal skeleton in **A**, *Nematonotus bottae* Pictet & Humbert, 49563, standard length *c.* 90 mm., Middle Cenomanian, Hakel, Lebanon; **B**, *Nematonotus longispinus* (Davis), P. 13882, standard length 114 mm., Middle Cenomanian, Hajula, Lebanon. In **C** are the bases of the upper caudal rays in P. 48825, *N. longispinus*, standard length 97 mm., to show the urodermal, *ud*. For explanation of other lettering see p. 102. In **B** the second uroneural is missing, in **A** and **C** arrows mark the outermost (unbranched) principal fin-rays.

of Hajula, Lebanon. There are no significant differences between these two species in the caudal region. In the specimen of *N. bottae* illustrated, the haemal arches of the third and fourth pre-ural centra are fused and the haemal spine of the third pre-ural centrum is partially doubled. This is an individual abnormality. As in *Aulopus* there is a large caudal scute (*f. s*) above and below the caudal skeleton and the neural spine of the second pre-ural centrum (*npu2*) is autogenous, spine-like and just over half as long as its predecessor. The autogenous haemal spines on the second and third pre-ural centra, three epurals (*er-3*), six hypurals (*hr-6*), long second ural centrum (*u2*, Fig. 25B) and second uroneural (*d2*) are as in *Aulopus*. The stegural (*st*) is forked proximally, with a process extending forwards on to the second pre-ural centrum. This process, absent in *Aulopus* and Ctenothrissiformes, is a primitive feature present in *Elops* and some clupavids (Patterson 1967a, fig. 11) which indicates the double origin of the first uroneural (Regan 1910 : 355; Patterson 1968 : 226). In *Nematonotus* there is a single urodermal (Fig. 25C), a structure absent from living myctophoids and Ctenothrissiformes but also present in the Cenomanian *Sardinioides attenuatus*. In *Nematonotus* the foremost procurrent caudal rays articulate with the neural and haemal spine of the third pre-ural centrum and the nineteen principal rays are preceded by four unsegmented and four segmented rays above, four unsegmented and two segmented rays below. In myctophoids the procurrent caudal rays are normally longitudinally divided, not spinous, but procurrent caudal spines appear in advanced members of the family Myctophidae (Fraser-Brunner 1949 : 1033).

III. DISCUSSION

(a) *The relationships of Ctenothrissiformes, Myctophoidei and Beryciformes.*

Monod (1967 : 118) has remarked that the structure of the caudal skeleton is rarely of value in discriminating between taxa at the generic level and below, but that it becomes increasingly valuable at the familial, subordinal and ordinal level. This observation is fully borne out by the forms described here, the only exception being the occurrence of two types of caudal skeleton in the ctenothrissiform family Aulolepididae, *Pateroperca* having the neural spine of the second pre-ural centrum fully developed, *Aulolepis* having it short and expanded, as it is in Ctenothrissidae. This suggests that *Aulolepis* and *Pateroperca* belong to different families, but *Pateroperca* is as yet so poorly known that no conclusion can be reached on this point until more specimens are discovered.

Among the Ctenothrissiformes, Myctophoidei and Beryciformes caudal anatomy is very similar. The basal type of caudal skeleton in these groups has the following features: the first pre-ural and ural centra fused, a free second ural centrum, three epurals, a stegural, a second uroneural and six hypurals (two lower and four upper). Caudal scutes above and below the caudal skeleton are present in *Aulopus*, most Cretaceous myctophoids (*Nematonotus*, *Acrognathus*, *Sardinioides*) and Ctenothrissiformes (*Aulolepis*, *Ctenothrissa*): they are absent in Beryciformes and higher groups. A single urodermal is present in *Nematonotus* and *Sardinioides attenuatus* among Cretaceous myctophoids. There is no urodermal in Ctenothrissiformes or Beryciformes. The main variations encountered in the caudal skeletons of myctophoids,

ctenothrissiforms and beryciforms involve reductions in the number of caudal elements by fusion or suppression and the condition of the neural spine of the second pre-ural centrum, which may be fully developed (*Pateroperca*, Polymixioidei, *Pycno-steroides*, *Dinopteryx*), spine-like and about half as long as its predecessor (*Nematonotus*, *Aulopus*, *Aipichthys*, *Pharmacichthys*), short and expanded (*Ctenothrissa*, *Aulolepis*, many myctophoids) or reduced to a low crest (Berycoidei).

The basal teleostean caudal skeleton, seen in such genera as *Leptolepis*, *Allothrissops*, *Thrissops*, *Ichthyodectes*, *Hiodon*, *Elops*, *Salmo*, etc., contains two free ural centra, three epurals, two lower hypurals and five upper hypurals (there may be six or seven upper hypurals in *Leptolepis*; Patterson 1968 : 220; there are only four in salmonids; Norden 1961 : 738), up to seven uroneurals (Patterson 1968) which extend forwards to the fourth pre-ural centrum in *Thrissops* and *Ichthyodectes*, to the third in *Leptolepis* and *Allothrissops* and to the second pre-ural centrum in *Hiodon*, *Elops*, *Salmo*, etc., and one or two urodermals (Patterson 1968 : 230). The condition of the neural arches and spines in the caudal region is often complicated by doubling of the segmental structures, usually as individual variations, but in *Leptolepis*, *Allothrissops*, *Elops* and some salmonids there is normally a neural arch and spine on the first pre-ural centrum, and in *Leptolepis*, *Hiodon*, osteoglossoids (Greenwood 1967) and *Alepocephalus* (Patterson 1968, fig. 12) there may be a more or less well developed arch and spine on the first ural centrum. It is usually assumed (e.g. Gosline 1961 : 14; Patterson 1967a : 104) that the second pre-ural centrum primitively bears a complete neural spine, supporting epaxial fin-rays. But among the forms described here the most primitive (*Aulopus*, *Nematonotus*) have the neural spine of the second pre-ural centrum about half as long as that of the third, and this is also true of *Elops* (Nybelin 1963, figs. 1, 4), which in other respects seems to be the most primitive living teleost. This suggests that the short second pre-ural neural spine may be primitive for some teleost groups. There are three possible conditions of the second pre-ural neural spine. It may be fully developed, as in *Allothrissops* (Patterson 1967a, fig. 6), *Ichthyodectes* (Cavender 1966, fig. 1), *Tarpon* (Nybelin 1963, fig. 7), and many other primitive teleosts, normally supporting epaxial fin-rays but in *Tarpon* ending just in front of the foremost epaxial fin-ray; it may be about half as long as its predecessor, as in *Elops*, "*Chupavus*" (Patterson 1967a, fig. 11), *Nematonotus* and *Aulopus*; or it may be represented only by a low crest, as in Berycoidei and generalized percoids (p. 87). Intermediates between the second and third of these conditions occur in *Aulolepis*, *Ctenothrissa* and many myctophoids. Intermediates between the first two conditions seem to occur only in primitive protacanthopterygian groups (salmonids, as in the specimen of *Cristivomer* illustrated by Vladkov 1954, fig. 2; characinids, as in the specimen of *Brycon* illustrated by Weitzman 1962, fig. 15) in which the pre-ural neural spines are very variable and both conditions may occur in a single species. The third condition, the spine reduced to a low crest, is undoubtedly advanced and may be left out of consideration here. In the ancestors of the teleosts, the pholidophorids, the neural spines of the last three pre-ural vertebrae decrease in size progressively so that all three end on approximately the same oblique plane: the first pre-ural neural spine is very short, the second is both shorter and more slender than the third (Patterson 1968, figs. 1-4). In pholidophorids

these neural spines do not reach the dorsal edge of the trunk and do not support fulcra or fin-rays. This condition of the pre-ural neural spines seems to be primitive for the teleosts as a whole and it persists in the Lower Jurassic *Leptolepis coryphaenoides* and *L. normandica* (Nybelin 1963, figs. 9, 10) and the Upper Jurassic *L. dubia* (Nybelin 1963, fig. 8; Patterson 1968, fig. 10). In the Upper Jurassic two of the three modern types of second pre-ural neural spine were already in existence. In *Allothrissops* and *Thrissops* (Nybelin 1963, figs. 11, 12; Patterson 1967a, fig. 6) both the second and third preural neural spines have elongated so that they reach the dorsal edge of the trunk, ending just in front of the foremost procurrent fin-rays: this is essentially the condition in living *Tarpon*. In the Upper Jurassic *Elops*-like fish illustrated by Nybelin (1963, fig. 6) the second pre-ural neural spine remains short but the third and fourth pre-ural neural spines are elongated, reaching the dorsal edge of the trunk and supporting the foremost procurrent fin-rays. This is essentially the condition in living *Elops*. There is no *a priori* reason to regard either of these two conditions as more primitive, both are a response to a new need, the necessity to support the epaxial procurrent rays as they extend forwards to increase the dorso-ventral symmetry of the tail. However, we know that the *Elops* type, with a short second pre-ural neural spine, has persisted unchanged in elopids since the Upper Jurassic and that this type of second pre-ural neural spine is primitive for the teleosts as a whole, and there is no reason for regarding the short neural spine of *Elops* and its Jurassic relative as a secondary regression from a long neural spine of *Tarpon* type. I conclude, therefore, that when one finds a second pre-ural neural spine resembling that of *Elops* in a generalized teleost one should regard it as a primitive feature unless there is good evidence to the contrary. In support of this interpretation is the occurrence of a second pre-ural neural spine of this type only in teleosts in which the caudal skeleton retains such primitive features as a free second ural centrum and nineteen principal caudal rays. A generalized teleost having an elongate second pre-ural neural spine is to be regarded as having developed this from a short spine of leptolepid or elopid type: this development can apparently take place spontaneously (see *Aipichthys*, Fig. 11).

From the basal type of teleostean caudal skeleton, the most primitive members of the myctophoid-ctenothrissiform-beryciform assemblage (such as *Nematonotus*) differ in the loss of one hypural, the seventh, whether by suppression or by fusion with the sixth is as yet unknown, have reduced the number of uroneurals to two, principally by loss of the small posterior uroneurals (ural neural arches 6-8), since the forked first uroneural of *Nematonotus* (Fig. 25) is clearly homologous with that of *Elops*, representing the second and third ural neural arches, while the second uroneural is probably homologous with the second uroneural of *Elops*, representing the fourth and fifth ural neural arches (Patterson 1968 : 226), the first pre-ural and ural centra have fused, and the first uroneural has fused with the first ural and pre-ural neural arches to produce a stegural, a development which took place very early in the protacanthopterygian lineage (salmonids, "*Clupavus*", etc.). These changes raise the question of the origin of the myctophoids and ctenothrissiforms. Greenwood *et al.* (1966 : 371) wrote of the ctenothrissiforms "we link them with some early group of myctophoid-like salmoniform fishes in which the supramaxillae were

not reduced, the premaxilla had not excluded the maxilla from the gape, and in which the adipose fin had disappeared." By extension, the ancestor of the myctophoids would be such a fish with an adipose fin. On the other hand, Gosline (1961 : 35; also Gosline, Marshall & Mead 1966 : 5) points out that the large caudal scutes of *Aulopus* make it impossible to derive the myctophoids from any living teleost except the elopoids. Weitzman (1967 : 532) discusses this point and notes that caudal scutes are present in *Argentina*, but the structures he describes in the salmonoid *Plecoglossus* and the galaxioid *Retropinna* do not seem to resemble caudal scutes. The absence in all known salmonoids of large caudal scutes and of a forked first uroneural of the type found in *Elops* and *Nematonotus*, together with the absence of recognizable salmonoids from pre-Tertiary rocks, make it difficult to envisage any direct relationship between salmonoids and myctophoids (Greenwood *et al.* 1966, fig. 1). A short second pre-ural neural spine resembling those of *Aulopus* and *Nematonotus* occurs in some salmonoids (*Coregonus*, which also has a urodermal), but the last few neural arches and spines and the epurals are apparently very variable, and no clear pattern emerges from Norden's (1961 : 738) analysis. In *Argentina* caudal scutes are present (though they are reduced) and the first pre-ural and ural centra are fused (Gosline 1960, fig. 10), as they must have been in the common ancestor of Myctophoidae and Ctenothrissiformes, but the neural spine of the second pre-ural centrum is elongate and supports procurrent fin-rays: in this character *Argentina* is advanced over the basal myctophoids and ctenothrissiforms. In the Clupeidae, a family with a fossil record extending back to the Upper Jurassic, large caudal scutes are usually present in the tail, the skull seems primitive enough to have given rise to both myctophoids and Ctenothrissiformes, and the caudal skeleton may be strikingly like that of *Nematonotus* (Patterson 1967a, fig. 11). It is unlikely that the known clupeids were ancestral to the myctophoids and ctenothrissiforms because of their reduced dentition and clupeid-like jaws, with a high coronoid process on the dentary, but they suggest a possible source for this type of caudal skeleton.

Taking the caudal skeleton of *Nematonotus* as the primitive condition for the myctophoids and ctenothrissiforms, the myctophoids are characterized by shortening and broadening the neural spine of the second pre-ural centrum, and in more advanced forms by fusion of the hypurals with each other and with the supporting centra. Within the ctenothrissiforms two distinct types of caudal skeleton occur: in *Ctenothrissa* and *Aulolepis* the neural spine of the second pre-ural centrum is expanded, as in myctophoids, tending towards the condition in Berycoidei and Percoidei; in *Pateroperca* the second pre-ural neural spine is fully developed, as it is in Polymixioidei. In *Aulolepis* and some species of *Ctenothrissa* there are procurrent spines in front of the caudal fin: this is specific evidence of evolution towards the Berycoidei and like the reduction of the second pre-ural neural spine in these fishes it distinguishes them from the Polymixioidei and Dinopterygoidei, in which procurrent caudal spines occur only in advanced forms.

Within the Berycoformes, the structure of the caudal skeleton gives some support to the division of the order into three suborders. In Polymixioidei there are always six hypurals and the neural spine of the second pre-ural centrum is fully developed. In Berycoidei the second pre-ural spine is reduced to a low crest (except in one

individual of *Monocentris*, Fig. 14), the procurent rays are spinous, and there are trends towards loss of the sixth hypural and fusion of the stegural and second ural centrum with the preceding centrum. In the Dinopterygoidei, already known to be a heterogeneous group, the neural spine of the second pre-ural centrum retains the primitive short condition (*Aipichthys*, *Pharmacichthys*) or is fully developed (*Dinopteryx*, *Pycnosteroides*) and there are trends towards loss of the sixth hypural. The polymixioid caudal skeleton (also found in *Dinopteryx* and *Pycnosteroides*) resembles that of the ctenothrissiform *Pateroperca*, differing only in having no caudal scutes and in having one less principal ray. The caudal skeleton of Berycoidei resembles those of *Aulolepis* and *Ctenothrissa*, differing only in having lost the caudal scutes and further reduced the second pre-ural neural spine. *Aipichthys* and *Pharmacichthys* seem to have the most primitive caudal skeletons known in Beryciformes, with nineteen principal rays, the primitive short second pre-ural spine, and, at least in some specimens of *Aipichthys*, six autogenous and separate hypurals and a free second ural centrum. Although both *Aipichthys* and *Pharmacichthys* are too specialized in other characters to have given rise to Beryciformes, their caudal skeleton could give rise to both the polymixioid condition (by elongation of the second pre-ural neural spine, which occurs spontaneously in some individuals of *Aipichthys*, Fig. 11C) and the berycoid condition (by shortening of the second pre-ural neural spine).

(b) *The origin of Perciformes.*

Gosline (1961a) discussed the caudal skeleton of Perciformes and found that the most generalized type contains fifteen branched principal rays, no neural spine on the second pre-ural centrum, three epurals, two free uroneurals, no free ural centra, five autogenous hypurals, and the haemal arches of the second and third pre-ural centra autogenous (see also Monod 1967, fig. 3). Gosline mentioned that this type of caudal skeleton occurs in *Kuhlia* (Kuhliidae), *Chaetodon* (Chaetodontidae), *Polydactylus* (Polynemoidei) and juvenile *Sphyaena* (Sphyaenoidei). Monod (1967) refers to this type of caudal skeleton as "sciaeno-sparidien banal" and states that it occurs in many Perciformes, mentioning *Sciaena* (Sciaenidae), *Pagrus*, *Sparus* (Sparidae) and *Gaterin* (Pomadasyidae). I find that this generalized type of caudal skeleton also occurs in *Centropomus* (Centropomidae), *Lateolabrax*, *Polyprion*, *Dicentrarchus*, *Morone*, *Acanthistius* (Percichthyidae, *sensu* Gosline 1966), *Branchiostegus* (Branchiostegidae), *Pomatomus* (Pomatomidae), *Brama* (Bramidae), *Arripis* (Arripidae), *Lutjanus* (Lutjanidae), *Nemipterus*, *Scolopsis* (Nemipteridae), *Lobotes* (Lobotidae), *Xenocys*, *Xenistius*, *Xenichthys* (Pomadasyidae), *Lethrinus*, *Sphaerodon* (Lethrinidae), *Monodactylus* (Monodactylidae), *Kyphosus*, *Medialuna* (Kyphosidae), *Ephippus*, *Drepane*, *Platax* (Ephippidae), *Chelmo*, *Heniochus*, *Pomacanthus* (Chaetodontidae), *Histioporus* (Pentacerotidae), *Cirrhitus* (Cirrhitidae) and *Schedophilus* (Stromateoidei). Many other groups, among them the Serranidae (*sensu* Gosline 1966), Cichlidae, Percidae, Acanthuroidei, etc. differ from this basal type only in the loss or incorporation in the stegural of the second uroneural. The occurrence of an apparently identical type of caudal skeleton in such a wide range of perciform groups, including forms with lunate, forked, emarginate and rounded caudal fins

in habitats ranging from pelagic to lacustrine, suggests that caudal anatomy is unlikely to contribute much to the unravelling of lineages among generalized Perciformes.

A caudal skeleton very similar to the basal perciform type occurs in some advanced Berycoidei (living Holocentridae and Diretmidae differ only in having the stegural fused with the underlying centrum (Fig. 20), Berycidae have the stegural fused with the centrum and also retain the sixth hypural (Regan 1911, fig. 1)) but here the hypurals support nineteen principal rays. In Myctophoidei a slightly different sequence of fusion is followed in which the second ural centrum partially retains its individuality. So far as I know, the basal perciform caudal skeleton is not precisely duplicated elsewhere.

The differences between the caudal skeleton and fin of basal Perciformes and those of generalized Beryciformes (*Polymixia*, *Aipichthys*, *Pycnosteroideis*, *Monocentris*) are:

(i) Reduction of the neural spine of the second pre-ural centrum. This has already taken place in all Berycoidei.

(ii) Fusion of the second ural centrum with the preceding two centra. This has taken place in most living Berycoidei and occurs in some individuals of *Aipichthys*.

(iii) Loss of the sixth hypural (the development of the caudal skeleton in *Mugil* and *Sphyræna* (Hollister 1937) suggests that Perciformes have lost the sixth hypural, not incorporated it in the fifth). This has already occurred in some individuals of *Aipichthys* and *Pycnosteroideis*, and takes place during the evolution of the Berycoidei (Holocentridae, *Diretmus*).

(iv) Reduction of the number of principal caudal rays from nineteen (Berycoidei, *Aipichthys* and *Pharmacichthys*) or eighteen (Polymixioidei, *Dinopteryx* and *Pycnosteroideis*) to seventeen.

(v) In all living Beryciformes, the foremost procurrent rays in each caudal lobe are true spines, but in Perciformes they are usually (? always) unsegmented lepidotrichia, with the right and left halves separate, and this is true of the earliest Perciformes (*Prolates*). In this character Perciformes are more primitive than living Beryciformes. Among Cretaceous Beryciformes, all Berycoidei, like their living relatives, have spines in front of the caudal fin; in Polymixioidei procurrent spines occur only in *Homonotichthys* and *Pycnosterinx dubius*, already known to be evolving towards the living *Polymixia* (Patterson 1964 : 301, 380), and in Dinopterygoidei they occur only in *Dinopteryx*. It is striking to find that spinous procurrent caudal rays occur only in those Cretaceous genera (except *Dinopteryx*) already known to be closely related to living Beryciformes.

The first of these five differences, the condition of the neural spine of the second pre-ural centrum, is the most interesting. As discussed above (p. 84) the primitive condition of this structure in teleosts seems to be as in *Elops*, *Aulopus* and *Nematonotus*, where the spine is slender and about half as long as its predecessor. This type of spine may elongate so that it supports procurrent fin-rays, as in Polymixioidei and many primitive teleosts, or it may become reduced to the percoid condition (Fig. 28). But apart from these two simple alternatives there are other possibilities which complicate the issue. First, the fully developed spine might become detached as an epural, producing the percoid condition direct. Secondly, from a low neural crest

of percoid type an apparent full neural spine might develop secondarily by fusion with the first epural. Thirdly, an apparent neural spine on the second pre-ural centrum might be produced by fusion between the second and third pre-ural centra. The last of these possibilities can normally be recognized by the partial or complete doubling of the neural or haemal spine on the compound centrum, as in *Pleuronectes* (Barrington 1937, fig. 1) and the specimen of *Saurida* illustrated by Weitzman (1967, fig. 18). The abnormal specimen of *Monocentris* illustrated in Fig. 14 is evidently a special case of this type of fusion, where the neural and haemal spines of the third pre-ural centrum are normally double and the posterior half of the neural spine has become attached to the succeeding centrum. This type of fusion does not seem of general significance in the present discussion.

Fusion of an epural with the neural crest of the second pre-ural centrum to produce a secondary neural spine (Fig. 28E) is a common occurrence in acanthopterygians: this process appears to account for the complete neural spine on the second pre-ural centrum in such groups as the Nandidae (but not *Pristolepis*; Gosline 1968, fig. 2b) among Percoidei, the Channiformes, Anabantoidei, *Luciocephalus*, some scombroids, pleuronectoid and soleoid pleuronectiforms, tetraodontiforms, etc. (Monod 1967; Liem 1963, 1967; Gosline 1968). In *Psettodes*, the most primitive living pleuronectiform, the caudal skeleton (Monod 1967, fig. 13) is of basal perciform type, with five autogenous hypurals and two uroneurals, but there is only one free epural and there appears to be a neural spine on the second pre-ural centrum. Monod identifies this spine as the first epural, for the element is partially or completely autogenous and the suture at the base lies not between the arch and the centrum but between the arch and the spine. *Psettodes* demonstrates clearly that the neural spine of the second pre-ural centrum in Pleuronectoidei and Soleoidei is an epural which has secondarily regained contact with and fused with a neural arch. That this has also occurred in scombroids such as *Neothunnus* can be seen by comparing figs. 15 and 16 of Monod (1967). A further peculiarity of the caudal skeleton of pleuronectoids and soleoids is that the parhypural tapers proximally and fails to make contact with the centrum (Monod 1967 : 117). The effect of this is to give dorso-ventral symmetry to the caudal skeleton, the free parhypural opposing the single epural just as the neural and haemal spines of the second pre-ural centrum oppose one another. A free parhypural, tapering proximally, also occurs in acanthopterygians such as the Channiformes (Monod 1967 : 117; Gosline 1968, fig. 2a), most Anabantoidei (Liem 1963 : 32), *Luciocephalus* (Liem 1967 : 114) and balistoids (Whitehouse 1910, pl. 50, fig. 33; Monod 1967 : 117), all forms with a neural spine on the second pre-ural centrum. Since none of these fishes has more than two epurals, all these groups appear to be cases of secondary fusion between the first epural and the second pre-ural neural arch in order to increase the dorso-ventral symmetry of the caudal skeleton. A complete neural spine on the second pre-ural centrum also occurs occasionally in basal percoids: Fig. 26 shows such a structure in a large specimen of *Siniperca* (Percichthyidae). In this individual there is a perfectly formed neural arch and spine (*npu2*) fully fused to the second pre-ural centrum, and there are only two epurals (*ei*, 2) compared with the three of normal *Siniperca*, most percichthyids and serranids. This specimen is best regarded as an abnormality foreshadowing the

fusion of the first epural with the second pre-ural neural arch in nandids, pleuronectiforms, etc.

It is thus well established that in many perciform groups and perciform derivatives the first epural can fuse with the second pre-ural neural arch. This raises the question of the homology of the perciform first epural: does the frequent fusion of this bone with the second pre-ural centrum indicate that these two structures were

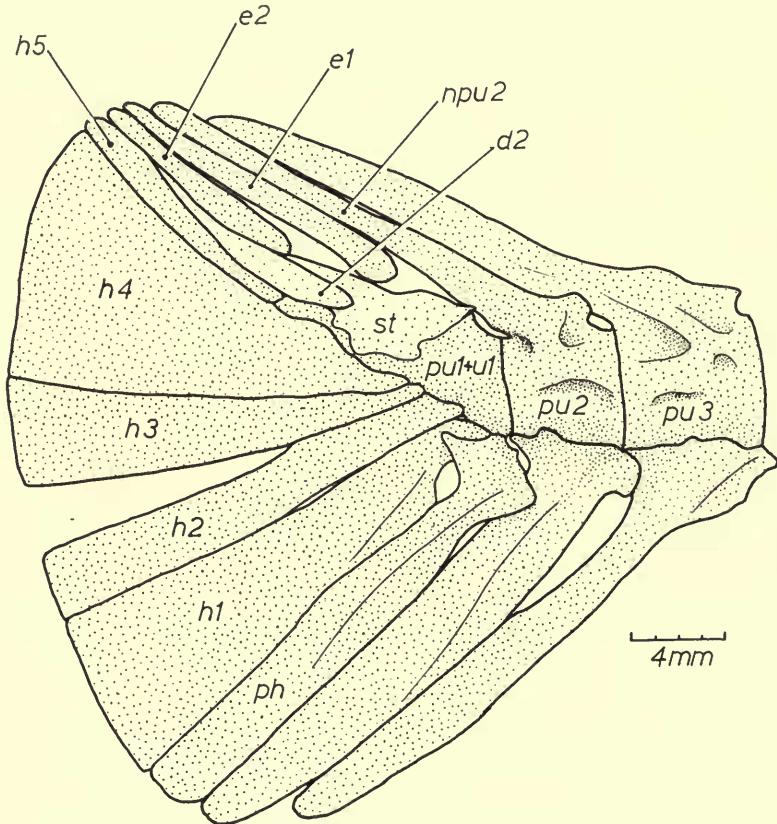


FIG. 26. *Simiperca chuatsi* (Basilewsky). The caudal skeleton of a dried skeleton showing a complete neural spine on the second pre-ural centrum, 1888.3.23.3, standard length 340 mm., Kiu Kiang, China. For explanation of lettering see p. 102.

originally part of the same segment? If so, the perciform first epural may have appeared by detachment of a fully developed neural spine in a caudal skeleton of polymixiid type. Rosen (1964 : 244) suggested that this took place in the evolution of the exocoetoids: that the ancestral exocoetoid had only two epurals and a fully developed neural spine on the second pre-ural centrum which became detached as the foremost of the three epurals in such a fish as *Dermogenys*. If this neural spine became detached in a fish which still retained the original three epurals one would expect there to be four epurals. Such a condition occurs very occasionally in

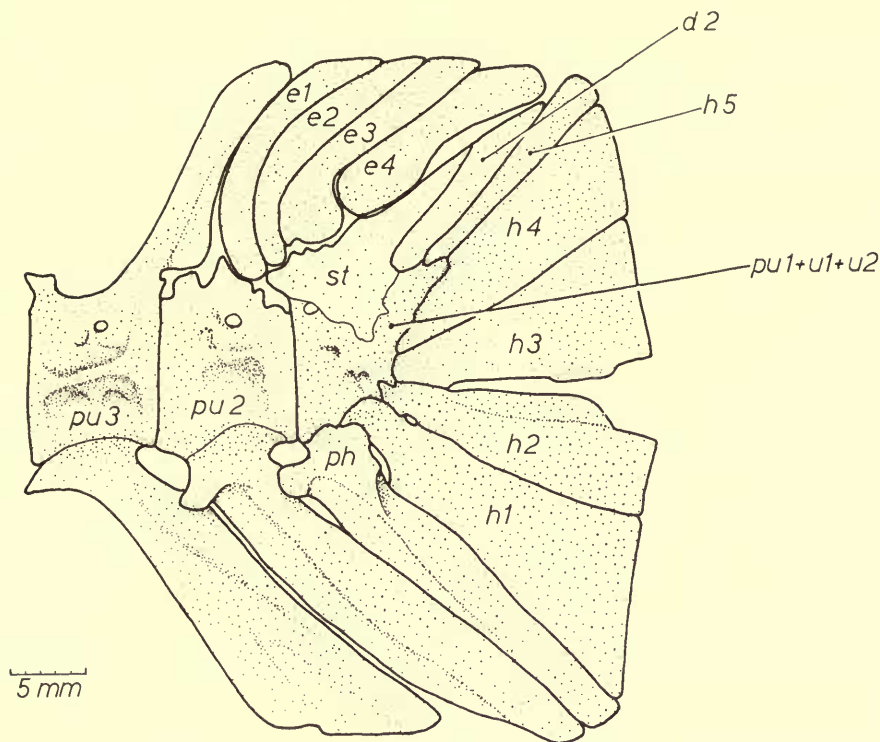


FIG. 27. *Pentaceropsis recurvirostris* (Richardson). Caudal skeleton of a dried skeleton showing four epurals, 1869.2.24.24, standard length 405 mm., Tasmania. For explanation of lettering see p. 102.

the generalized percoid caudal skeleton, as in the individual of *Pentaceropsis* (Pentacerotidae) shown in Fig. 27.

The epurals of teleosts are the remnants of a more numerous set of bones in primitive actinopterygians which are serial homologues of the supraneurals above the anterior vertebrae, and like these bones they were primitively metameric (Patterson 1968 : 221), but the metameric arrangement of the epurals has been lost in living chondrosteans. In the most primitive teleosts, such as the Jurassic *Leptolepis* and *Allothrissops* (Patterson 1967a, figs. 3, 6), the three epurals still show an apparent metamery, suggesting that they represent the neural spines of the first pre-ural neural arch and two ural neural arches: this seems to be supported by conditions in osteoglossoid fishes, where there are often fully-developed neural spines on both the first pre-ural and the first ural centra, and where there is never more than one epural (Greenwood 1967). But in higher teleosts, as in living chondrosteans, a metameric arrangement of the epurals is no longer recognizable. At the percoid level, for example, one can find fishes with all the epurals behind the neural crest on the second pre-ural centrum (Gosline 1961a, fig. 1, *Kuhlia*; 1968, fig. 5c, *Bathymaster*), or with one epural above the crest (Gosline 1961a, fig. 2, *Parupeneus*; Hollister 1937,

figs. 12-14, *Sphyræna*) or with two above it (Hollister 1937, fig. 8, *Mugil*). Further, in groups such as the Berycoidei and Percoidei there is good evidence that in primitive forms the first epural lies behind the neural crest of the second pre-ural centrum, moving forwards above it in more advanced forms (in berycoids cf. Figs. 17, 21 with Figs. 13, 20). Since there is no evidence that strict metamery of the epurals is maintained in acanthopterygians there is no reason to believe that the perciform first epural is the detached neural spine of the second pre-ural centrum. The individual of *Pentaceroopsis* shown in Fig. 27 is best interpreted merely as exhibiting a supernumary epural: such a condition is already known to occur in the salmonid *Oncorhynchus*, where Vladykov found four epurals in three out of 1,020 specimens (1962, table 8).

The conclusions drawn from this discussion of the second pre-ural neural arch and spine are that the low neural crest in basal percoids is to be regarded as having evolved by reduction of the primitive short neural spine, and that the ancestors of the perciforms are to be found among fishes having a low crest or short neural spine on the second pre-ural centrum, not among those with a full neural spine. Where there is a full neural spine on the second pre-ural centrum in Perciformes and perciform derivatives, it is to be regarded as having arisen by fusion of an epural with a low neural crest. These conclusions are illustrated in Fig. 28.

With this background on the perciform caudal skeleton, we can now consider the evidence of caudal structure in the various beryciform-perciform lineages that have been suggested (Patterson 1964). These were, in decreasing order of confidence,

Polymixiidae (<i>Omosoma</i> — <i>Berycopsis</i> lineage)	—————>	Scorpididae, Monodactylidae and Kyphosidae
Aipichthyidae	—————>	Carangidae
Pharmacichthyidae	—————>	Acanthuroidei
Sphenocephalidae	—————>	basal Percoidei (Serranidae, etc.)
Pycnosteroididae	—————>	Chaetodontidae
Dinopterygidae	—————>	Centrarchidae

Detailed study of the caudal skeleton cannot be said to give support to these lineages. Of the various perciform groups mentioned, the scorpidids, monodactylids, kyphosids, basal percoids (*Centropomidae*, *Percichthyidae*), *Chaetodontidae* and *Centrarchidae* have the generalized percoid type of caudal skeleton, differing from those of Beryciformes in the characters listed on p. 88. The acanthuroids are more advanced only in having lost the second uroneural, while the carangids have enlarged the first epural and show fusion between the first and second hypural and between the third and fourth hypurals. Among the beryciform groups, the polymixiids, sphenocephalids, pycnosteroidids and dinopterygids all have a complete neural spine on the second pre-ural centrum: for reasons given in the discussion above, it is unlikely that a percoid caudal skeleton can be derived directly from this condition. In *Sphenocephalus* there are only two epurals, suggesting the possibility

of arriving at a percooid arrangement of three epurals and a low neural crest on the second pre-ural centrum by detachment of the neural spine on this centrum, but further study of *Sphenocephalus* has yielded strong evidence (to be discussed in a forthcoming paper by the author and D. E. Rosen) that far from being an ancestral percooid it is related to the percopsiforms. In the aipichthyids and pharmacichthyids

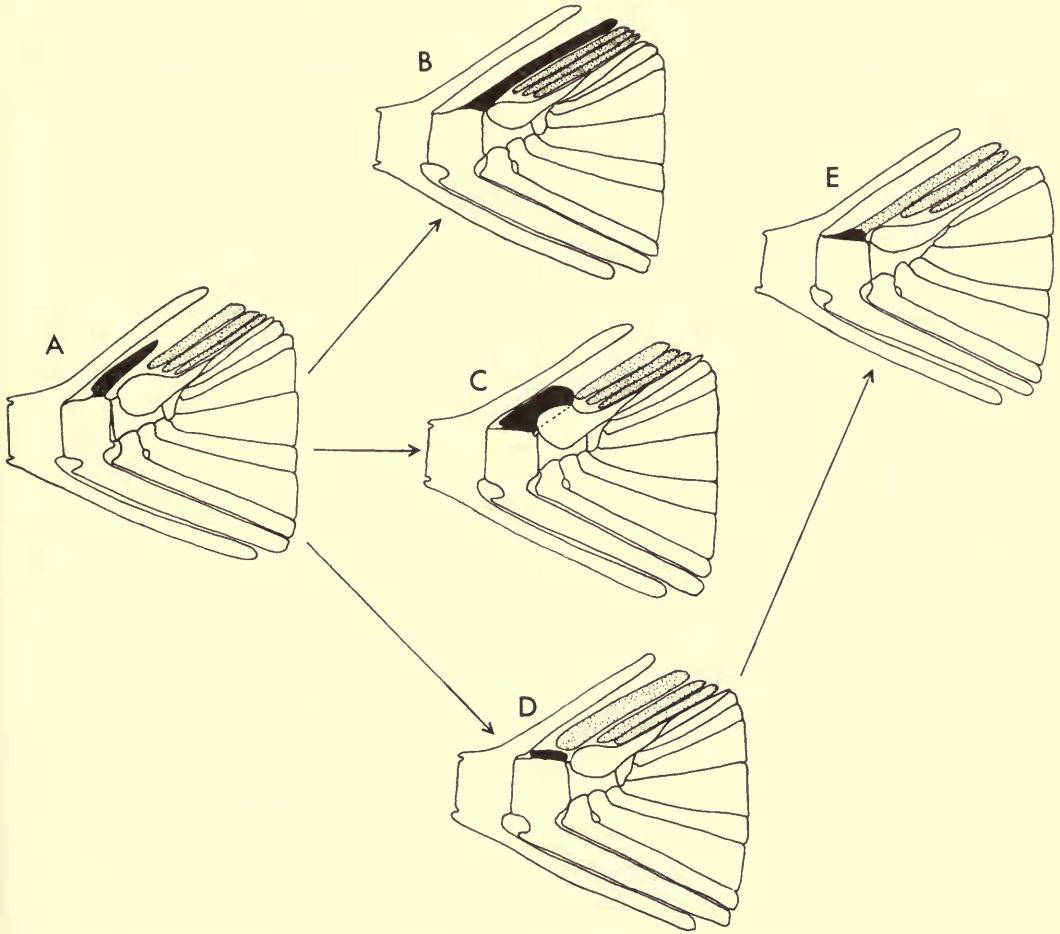


FIG. 28. Diagrams to show changes in the second pre-ural neural spine (black) in the evolution of the myctophoids, ctenothrissiforms and acanthopterygians. **A**, the primitive short neural spine, as in *Nematonotus*, *Aulopus*, *Aipichthys* and *Pharmacichthys*; **B**, elongation of the neural spine to support procurrent fin-rays, as in *Pateoperca*, *Polymixiidae*, *Dinopteryx* and *Pycnosterooides*; **C**, expansion of the neural spine into a plate, as in most myctophoids, *Ctenothrissa*, *Aulolepis* and some primitive Berycoidei; **D**, reduction to a low crest, with the first epural (stippled) moving forwards above it, as in most Berycoidei and Perciformes (a berycooid is illustrated); **E**, production of a secondary neural spine by fusion of the first epural in fishes with no free second ural centrum and five hypurals, as in Zeiformes (except Caproidae), Nandidae, Channiformes, Anabantoidae, Pleuronectiformes, etc.

the neural spine of the second pre-ural centrum is still short, as in the most primitive teleosts, and could give rise to the percoid condition by reduction. Further, in *Aipichthys* (Fig. 11) there is a tendency to reduce the number of hypurals to five and also to fuse the second ural centrum into the preceding centrum, as in percoids. There seems to be nothing in the caudal skeleton of *Aipichthys* to oppose the postulated link with the carangids. In *Pharmacichthys* the caudal skeleton is like that of *Aipichthys*, so far as it is known, and the fin-rays are deeply cleft basally, as in carangids: this character reduces the possibility of a relationship between *Pharmacichthys* and the acanthuroids and balistoids, in which the caudal fin-rays are unmodified.

Except for the *Aipichthys*-carangid lineage, the evidence of the caudal skeleton indicates that Gosline's (1966a) criticism of the polyphyletic scheme of perciform origins which I proposed are well founded. But the evidence on which Gosline based these criticisms, the structure of the supraoccipital crest, does not in fact oppose the various beryciform-perciform lineages. Gosline (1966a : 412) contrasted the type of supraoccipital crest seen in the polymixiids *Homonotichthys* and *Polymixia*, and in the carangids, priacanthids, etc., which extends forwards between the frontals, is knife-edged and buried in musculature, with the type of crest seen in *Antigonia*, acanthuroids, chaetodontids, etc., which is short, high and thickened anteriorly, extending "up and back over the nape as a sort of protective shell". Gosline finds that these two types of supraoccipital crest are "structurally and functionally . . . far apart", and writes "nor does it appear that one could be developed from the other except by going all the way back through some intermediate form with a relatively small, unspecialized occipital crest". Gosline draws the conclusion that *Aipichthys* and *Sphenocephalus*, both with a short crest, thickened anteriorly, could not have given rise respectively to the carangids and serranids, which have a long, knife-edged crest. But the evolution of the Berycoidei shows (as clearly as such processes can be shown by the fossil record) that fishes with a short "*Aipichthys*-type" crest can give rise to fishes with a long "carangid-type" crest. The most primitive Berycoidei have an "*Aipichthys*-type" crest, moderately high and thickened anteriorly: this is true of both the trachichthyid lineage (*Lissoberyx*, Patterson 1967, fig. 2) and the holocentrid lineage (*Caproberyx*, Patterson 1964, fig. 67; 1967, fig. 10, *Stichocentrus*, Patterson 1967, fig. 8). From this basal type there are in berycoids two divergent trends in the evolution of the supraoccipital crest. In Holocentridae the frontals grow backwards, partially covering the parietals, eliminating the supratemporal fossa, and producing a low supraoccipital crest which secondarily comes to resemble the small supraoccipital crest of primitive teleosts. In Trachichthyidae (*Hoplopteryx*, *Hoplostethus*) the supratemporal fossa extends forwards and the supraoccipital crest becomes elongated, thickened centrally and knife-edged. This trend continues further in the Berycidae, and *Beryx* has a long knife-edged crest, continued forwards by the frontals above the orbit, which resembles those of *Polymixia* and the carangids. If a "carangid-type" supraoccipital crest developed from an "*Aipichthys*-type" within the Berycoidei, there is no reason why these changes could not have occurred in other lineages.

It should also be mentioned here that Gosline (1966a : 410) has indicated that Beryciformes differ from Perciformes in the number of infraorbitals and the extent of the subocular shelf. He finds that in Beryciformes (except Holocentridae) there are four circumorbitals behind the lachrymal whereas in Perciformes there are five, and that in Beryciformes the subocular shelf extends over more than one infraorbital while in Perciformes it is confined to the second infraorbital. The subocular shelf extends along all the infraorbitals in Holocentridae (living and fossil) and in Polymixiidae (*Polymixia*, *Homonotichthys*), but in Trachichthyidae (living and fossil), Berycidae, Monocentridae, etc., the shelf is restricted to the second infraorbital, as in Perciformes. The subocular shelf also extends along all the infraorbitals in Anabantidae and Belontiidae (Liem 1963): probably a subocular shelf on all the infraorbitals, as in polymixiids, holocentrids and anabantids, is the primitive condition of the structure (Smith & Bailey 1962 : 3). In the number of infraorbitals the basic beryciform condition is undoubtedly as in percoids, with a total of six bones, a lachrymal, four infraorbitals, and a dermosphenotic overlying the autosphenotic: this condition occurs in Polymixiidae, living and fossil, and in living Holocentridae. In Trachichthyidae, Berycidae, Monocentridae and some Cretaceous Holocentridae (*Caproberyx*, *Stichocentrus*, Patterson 1964 : 347; 1967 : 89) the apparent reduction in number of circumorbital bones is caused by fusion of the dermo- and autosphenotics, which had already occurred in the Cretaceous trachichthyid *Hoplopteryx* (Patterson 1964, fig. 55).

In summary, of the various beryciform-perciform lineages which have been proposed, only the *Aipichthys*—carangid lineage emerges unscathed from a detailed examination of caudal structures. The caudal skeletons of Polymixiidae, *Sphenoccephalus*, *Dinopteryx* and *Pycnosteroides* differ fundamentally from those of Perciformes in having a full neural spine on the second pre-ural centrum. In *Aipichthys* and *Pharmacichthys* there are tendencies towards the Perciformes in the occasional fusion of the second ural centrum with the preceding centrum and the occurrence of five hypurals, but it is only among the Berycoidei that the basal perciform caudal skeleton is duplicated. All known Berycoidei, even the very generalized *Lissoberyx*, are more specialized than Perciformes in having procurrent caudal spines, and this and characters of the skull (Patterson 1964 : 467) show that no perciform could have evolved from any known berycoid. But if the Perciformes and cognate groups (Channiformes, Scorpaeniformes, Pleuronectiformes, Tetraodontiformes) should prove to be a monophyletic group, an alternative to the traditional method—"an attempt first to define orders and other higher taxa and then to speculate upon their origin, albeit in the light of the known fossils" (Greenwood *et al.* 1966 : 346) is to use the criteria recommended by Hennig (1966 : 88, 120) and to search among the living fauna for the sister group (Hennig 1966 : 139; see also Brundin 1966 : 17) of this assemblage. A preliminary analysis suggests that the Berycoidei, not the Beryciformes as a whole, may fill this role. This is indicated not only by features of the caudal skeleton but by the fact that the Berycoidei is the only beryciform group showing such perciform features as a subocular shelf confined to the second infraorbital, the absence of epineurals, the pelvic girdle firmly joined to the cleithra (in Berycidae especially), pelvic fins containing a spine and five soft rays (in Anomalo-

pidae and Gibberichthyidae, for example), partially separate soft and spinous dorsal fins, etc., and in the stephanoberycoids, which appear to be merely specialized offshoots of the trachichthyid lineage, loss of the orbitosphenoid. While it is clear that many of these perciform characters in Berycoidei have arisen independently within the group and were not inherited from a common ancestor of Berycoidei and perciforms, they appear to be true parallelisms (Simpson 1961 : 78), and are indicative of relationship.

(c) *Intermediate groups.*

Between the Beryciformes and the basal Percoidae, Greenwood *et al.* (1966 : 398) place the Zeiformes, Lampridiformes, Gasterosteiformes, Channiformes, Synbranchiformes, Scorpaeniformes, Dactylopteriformes and Pegasiformes. Of the Gasterosteiformes, Scorpaeniformes, Dactylopteriformes and Pegasiformes I have nothing to say. The Channiformes (see Gosline 1968) and Synbranchiformes are probably derived from the percoid level rather than from the beryciform or pre-beryciform.

In Zeiformes the caudal skeleton resembles those of basal Perciformes in having no free second ural centrum and in having only five hypurals, and is more advanced than basal percoids in having lost the second uroneural. In Zeidae (*Zeus*, *Cyttus*), Oreosomatidae (*Neocyttus*) and Grammicolepidae (*Xenolepidichthys*) there is a complete neural spine on the second pre-ural centrum, but this never occurs in conjunction with three epurals, and in Caproidae (*Capros*, *Antigonia*; Gosline 1961, fig. 4A), which in other respects appear to have the most primitive caudal skeletons of the group (the hypurals autogenous, the stegural autogenous in *Antigonia*) there are three epurals and there is a low crest on the second pre-ural centrum, as in percoids. Conditions in the Caproidae indicate that the neural spine on the second pre-ural centrum in Zeidae, Oreosomatidae and Grammicolepidae has arisen secondarily by fusion of the first epural (see above, p. 89, Fig. 28), and that as Gosline (1961) has already said, there is nothing in the caudal skeleton to distinguish Zeiformes from Perciformes. It has long been recognized that the Zeiformes are probably related to the Beryciformes, principally because of the pelvic ray count, but they also show many perciform features (Gosline 1961 : 36) and no conclusion has yet been reached on whether they are more closely related to the beryciforms or the perciforms, although in most recent classifications they are placed directly after the Beryciformes. Stinton (1967) has recently shown that there is a remarkable resemblance between the otoliths of *Antigonia* and those of Berycoidei (Berycidae, Trachichthyidae, and especially Monocentridae). Stinton interprets this as indicating that *Antigonia* is a berycoid, for he finds that the otoliths of *Capros* resemble those of the zeids rather than *Antigonia*. However, the evidence that *Antigonia* and *Capros* are related can hardly be ignored, and in Stinton's illustrations of zeiform otoliths it seems possible to recognize a trend in reduction and specialization of the otolith in the sequence *Antigonia-Capros-Cyttus-Zeus*: the same sequence of increasing specialization is also shown by fusion within the caudal skeleton. In my opinion Stinton's otolith evidence indicates not that *Antigonia* is a berycoid, but that as the most primitive living zeiform it retains the clearest evidence of a common ancestry with the Berycoidei. The percoid-like caudal skeleton, pelvic spine, etc., of the

Zeiformes do not oppose such a relationship. In Hennig's terminology, the Zeiformes appear to be the apomorph sister group of the Berycoidei, these two groups together forming the plesiomorph sister group of the perciform assemblage (see above, p. 95).

The Lampridiformes, previously unknown before the Oligocene, have recently acquired a respectable fossil record with Bonde's (1966) preliminary description of a ? veliferid from the basal Eocene Mo-clay of Denmark, his opinion that *Palaeocentrotus* Kühne (1941), from the same beds, is a lampridoid, not a zeiform, and the suggestion (p. 81) that the Danian *Bathysoma* is a lampridiform, not a menid. It appears that the deep-bodied Lampridiformes of the suborder Lampridoidei were an important element of early Tertiary faunas. The caudal skeleton of Lampridiformes (known in *Velifer*, *Lampris*, *Palaeocentrotus* and *Bathysoma*) is characterized by fusion of one or more of the upper hypurals with the second ural centrum, but in other respects it does not differ from that of Beryciformes (there are six hypurals in *Velifer*). In *Lampris* and *Velifer* the neural spine of the second pre-ural centrum is reduced, but in *Palaeocentrotus* (Kühne 1941, fig. 2) it is about half as long as its predecessor, a primitive condition only found among Beryciformes in *Aipichthys* (Fig. 11) and *Pharmacichthys*. Further, in *Lampris* and *Velifer* there are seventeen branched caudal rays and the caudal rays are deeply cleft basally, covering much of the hypurals. These points tend to confirm the suggestion (Patterson 1964 : 473) that the Lampridiformes are an offshoot of the Dinopterygoidei. Within the Dinopterygoidei, the second pre-ural neural spine, the seventeen branched principal rays, the "hypurostegy" and the absence of a pelvic spine all point to the Aipichthyidae and Pharmacichthyidae as ancestral forms.

Transference of *Bathysoma* to the Lampridiformes leaves unsettled the position of *Mene*, to which I thought *Bathysoma* was related (Patterson 1964 : 424). The similarities between *Mene* and *Bathysoma* are numerous, and extend to the form of the fin-rays, which are preserved in the middle part of the anal fin of the holotype of *B. lutkeni* in Copenhagen, and are short, broad and unbranched (Bonde, personal commn). The skull of *Mene* is also strikingly like that of *Velifer* (Regan 1907, figs. 167, 169). But the caudal skeletons of *Mene* and the Lampridiformes are very different. The six hypurals (in *Velifer*), fusion of the second ural centrum with the upper hypurals rather than with the preceding centrum, and the seventeen branched principal rays of Lampridiformes can only be derived from beryciform or pre-beryciform ancestors, but the caudal skeleton of *Mene*, with fifteen branched principal rays and fusion of the second ural centrum and first four hypurals with the preceding centrum could have evolved from the caudal skeleton of basal percoids (p. 81). Nor can I find anything in the skull and vertebral column of *Mene* which is against perciform ancestry. Nevertheless, *Mene* has an unusually long fossil record, extending back to the Lower Palaeocene. The earliest recorded species, *M. phosphaticus* Astre (1927) from the Montian of Tunisia, seems to agree with *Mene* rather than with the Lampridiformes in caudal structure. *Mene* is very common in the Middle Eocene of Monte Bolca: with *Mene* at Monte Bolca there occur other deep-bodied fishes of similar structure such as *Exellia* (= *Semiophorus*). These fishes, though poorly known, seem to agree with *Mene* in the absence of spines

in the dorsal and anal fins (see Blot 1967 on *Exellia*) and also in the deeply cleft bases of the caudal fin-rays. It is difficult to know how much significance can be attached to this last character. E. & Y. Le Danois (1964), who coined the term "hypurostegy" for it, give great importance to it and use it to unite in an "ordre des Sombres" fishes as diverse as the holostean Pachycormidae, the Cretaceous Tselfatiidae, the lampridiform Veliferidae and Lampridae, the carangids, scombrids and others. In my opinion this assemblage is entirely spurious; the occurrence of hypurostegy in such varied groups indicates not that the fishes are related but that hypurostegy has arisen independently in a number of lines, for reasons as yet unknown. E. & Y. Le Danois made a new family Vomeridae to include *Mene*, the Eocene *Vomeropsis*, and the deep-bodied carangids *Vomer*, *Selene*, *Alectis* and *Hynnix*, grouping this family with the Lampridae, Veliferidae, Ehippididae and *Exellia*. Although the reasoning on which this grouping is made is doubtful, there may be some truth in it. It seems possible that *Mene* and *Exellia* could represent an independent attainment of the perciform grade from the Palaeocene lampridiform stock. But the possibility that the resemblances between these Eocene forms and the Lampridiformes are due to convergence is by no means ruled out: revisionary studies on the Monte Bolca fauna now in progress (Blot 1967) may settle this question.

IV. CONCLUSIONS

Study of a single structural complex such as the caudal skeleton is unlikely to produce firm conclusions on matters of phylogeny and relationships. Rather it will serve as a means of checking existing hypotheses and will raise questions to be settled by more comprehensive work. The main points arising from this paper are as follows. An asterisk indicates that the genus or group is extinct.

1. Ctenothrissiformes,* Myctophoidei and Beryciformes have a basically similar caudal skeleton, with the first ural and pre-ural centra fused, a free second ural centrum, a stegural (the first uroneural fused with neural arch material from the first ural and pre-ural centra), a second uroneural, three epurals and six hypurals. The primitive nineteen principal caudal rays are retained in all ctenothrissiforms and myctophoids, and in all beryciforms except the Polymixiidae, Sphenocephalidae,* Dinopterygidae* and Pycnosteroididae,* which have eighteen.

2. Ctenothrissiformes* (*Aulolepis*, *Ctenothrissa*) and Myctophoidei (*Aulopus*, *Nematonotus**, *Sardinioides**, *Acrognathus**) have a large caudal scute above and below the caudal skeleton. The myctophoids *Nematonotus** and *Sardinioides attenuatus** have a single urodermal on the base of the upper caudal rays. Both caudal scutes and urodermals are relict structures absent in all higher groups.

3. The neural spine of the second pre-ural centrum in teleosts is primitively slender and about half as long as its predecessor, as in *Elops* and *Leptolepis*.* This type of second pre-ural neural spine persists in the myctophoids *Aulopus* and *Nematonotus** and in the beryciforms *Aipichthys** and *Pharmacichthys*.* In Ctenothrissiformes,* *Ctenothrissa* and *Aulolepis* have this short spine expanded into a plate, as it is in most myctophoids, but in *Pateroperca* the spine is elongate and supports procurrent fin-rays. A fully developed second pre-ural neural spine also occurs among Beryciformes in all polymixioids (Polymixiidae, Sphenocephalidae*) and in the dinop-

terygoids *Dinopteryx** and *Pycnosteroides*.* In Berycoidei, as in generalized Perciformes, the second pre-ural neural arch and spine are reduced to a low crest.

4. The differences between the caudal skeletons of Myctophoidei and Ctenothrissiformes* and those of the most primitive teleosts are minor. Among primitive teleosts the Clupavidae* come closest to the Ctenothrissiformes and Myctophoidei in caudal anatomy.

5. The foremost procurrent caudal fin-rays are spinous in all living Beryciformes. This is a feature peculiar to Beryciformes: Perciformes appear to be without procurrent caudal spines. Procurrent caudal spines also occur in some species of *Ctenothrissa* and in *Aulolepis* (Ctenothrissiformes*), probably an indication of relationship between Ctenothrissiformes and Beryciformes, although procurrent caudal spines have also developed in advanced members of the myctophoid family Myctophidae. Among Cretaceous Beryciformes, procurrent caudal spines occur only in forms already known to be closely related to living Beryciformes (all Berycoidei and the polymixiids *Homonotichthys** and *Pycnosterinx**) and in *Dinopteryx*.*

6. Within the Beryciformes, the principal variations in the caudal skeleton and fin (apart from those in the second pre-ural neural spine, principal fin-ray count and procurrent fin-rays already mentioned) are the presence of only two epurals in *Sphenocephalus** (Polymixioidei), the presence of only five hypurals in *Aipichthys velifer**, some specimens of *Pycnosteroides** (both Dinopterygoidei) and in many Berycoidei (living holocentrids, *Diretmus*), and the fusion of the second ural centrum with the preceding centrum in some specimens of *Aipichthys** and in many Berycoidei (Berycidae, Diretmidae, Anoplogasteridae, living Holocentridae). A full neural spine on the second pre-ural centrum has been found in one individual of *Aipichthys** and one of *Monocentris*, simulating the polymixoid condition.

7. The basal perciform caudal skeleton differs from the basal beryciform type in having only five hypurals, no free second ural centrum and only seventeen principal rays. Perciformes are primitively characterized by having a low neural crest on the second pre-ural centrum. Where a complete second pre-ural neural spine occurs as a normal feature in perciform or higher groups the condition is secondary, the spine representing an epural which has secondarily fused with the neural arch.

8. Evidence from the caudal skeleton does not support the various independent beryciform—perciform lineages which have been proposed. The polymixioids and the dinopterygoids *Dinopteryx** and *Pycnosteroides** differ fundamentally from the various perciform groups which they otherwise resemble in having a fully developed neural spine on the second pre-ural centrum. *Pharmacichthys**, which resembles the acanthuroids and balistoids in many ways, differs from them in having the bases of the caudal fin-rays deeply cleft, and is therefore unlikely to have been ancestral to these groups. Only the postulated link between *Aipichthys** and the carangids is not opposed by evidence from the caudal skeleton and fin.

9. Although no known berycoid could have been ancestral to any perciform, the Berycoidei is the only beryciform group in which the caudal skeleton evolves towards the percoid condition. There are many other characters and evolutionary trends in which the Berycoidei is the only beryciform group to resemble the percoids: these suggest that the Berycoidei is the sister group of the Perciformes and cognate groups.

10. The caudal skeleton shows that the Danian *Bathysoma** is a lampridiform (the earliest yet known), not a member of the Menidae. It is suggested that the Lampridiformes originated from near the beryciform families Aipichthyidae* and Pharmacichthyidae.* In the Eocene there are fishes (*Mene*, *Exellia**) which have reached the perciform grade but resemble the Palaeocene and Eocene Lampridiformes: possibly these forms represent an independent attainment of the perciform grade from lampridiform ancestors.

11. The caudal skeleton of the Zeiformes is basically of percoid type, but the evidence of zeiform otoliths indicates that they are closely related to the Berycoidei. The Zeiformes is evidently the sister group of the Berycoidei, these two groups together being the sister group of the perciform assemblage.

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VI. ABBREVIATIONS USED IN FIGURES

<i>d</i> ₂	second uroneural
<i>e</i> 1-3	epurals
<i>f.s</i>	caudal scute
<i>h</i> 1-6	hypurals
<i>hpu</i> ₂	haemal spine of second pre-ural centrum
<i>npu</i> ₂ , <i>npu</i> ₃	neural spines of second and third pre-ural centra
<i>ph</i>	parhypural (haemal spine of first pre-ural centrum)
<i>pu</i> ₁ + <i>u</i> ₁	centrum formed by fusion of first pre-ural and ural centra
<i>pu</i> ₂ , <i>pu</i> ₃ , <i>pu</i> ₄	second, third and fourth pre-ural centra
<i>st</i>	stegural (first uroneural fused with pre-ural neural arch material)
<i>u</i> ₂	second ural centrum

Combinations of symbols linked by plus signs indicate compound elements formed by fusion of the bones indicated.

